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Migration and natal dispersal in the barn swallow *Hirundo rustica*

Ph.D. Thesis

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GENERAL INTRODUCTION

Introduction

A detailed knowledge of all different phases of the annual cycle is fundamental to fully understand the ecology of a population (Newton 2008). Birds, and particularly species that migrate over long-distances, spend their life on the wing, crossing and staging in many areas, often in different continents, at different times of the year. Each of these steps in the circannual life cycle requires that birds take decisions on where to settle and breed, on which route to follow in order to reach hospitable wintering grounds, how long to stay and when to depart from the individual areas they temporarily inhabit. Such decisions are made by naïve individuals in their first year of life and are possibly reiterated in the following years. Hence, migratory species have to cope with different habitats, with different abiotic conditions, as well as, for example, predators, competitors and parasite faunas which may exert divergent selection on the same life history traits. Moreover, every single decision may entail carry-over effects that are expressed later in life, and can have additional impact on individual fitness. These effects on fitness of individuals will ultimately translate into consequences at the population level, thereby determining population dynamics and trends.

1.1 Migration

Migration and dispersal are the two main large-scale movements birds are capable of (Newton 2008). Migration is defined as a seasonal return movement in fixed directions between separate breeding and wintering ranges; many animal species of disparate taxa have evolved the ability to migrate in order to better cope with seasonal variation in environmental conditions. However, birds are the taxon where migration has evolved to its maximum expression.

Unlike migration, dispersal is defined as a one-way movement. In both sedentary and migratory bird species, after becoming independent of their parents, juveniles disperse in various directions from their natal site; this movement, called natal dispersal, contributes to population dynamics and genetic structure and can be measured by the distance between natal sites and the site where the individual will eventually settle to breed for the first time. Natal dispersal and settlement to breed may be followed by subsequent breeding dispersal, whereby an individual moves between sites to breed in consecutive years or even between breeding events in the same breeding season. Thus, breeding dispersal is expressed by the distance between consecutive breeding sites (Newton 2008).

A typical migratory bird from temperate and boreal latitudes, once out of the nest and before starting the autumn migration south, will possibly explore the surroundings of its natal place, prospecting for suitable places where to settle to breed for the first time. Several factors may affect the final decision on natal dispersal already at this stage. Body size, and particularly the flight apparatus, and general physiological state will influence exploratory behaviour and thus the number of potentially suitable sites that a disperser will visit. Habitat structure and social factors, including the density of conspecifics but also the density of competitors, will cause variation in dispersal or may constrain prospecting opportunities.

Finally, interactions with close kin will affect the fitness payoff of any dispersal decision by influencing the risk of inbreeding and of competing with kin for limiting resources, including mates. During the autumn migration it must be decided where to do stopover, where to winter and, after the spring migration, where to set. Year after year, survivors will have the opportunity of capitalizing on previous experience, in order to use the same staging and wintering sites or to change their strategy.

Obviously, knowledge of migration and wintering decisions is pivotal in the evolutionary study of behaviour and ecology of bird populations, but also for their conservation. This is the case because analysing the mechanisms that influence migration and wintering decisions can improve our understanding of the consequences that environmental change will have on population dynamics, but also because it allows to devise ad hoc conservation actions that can mitigate any negative population trends by silencing the factors that are jeopardizing the focal populations of interest. Thus, knowledge of both migration and dispersal and tracking migratory animals between across stages of their annual cycle, understanding how events at different stages of the life-cycle interact and the mechanisms controlling these movement and decisions are all necessary elements of our knowledge of the ecology of migrant species and of the mechanisms of population dynamics.

Particularly long-distance migrants, which are sensitive indicators of environmental conditions on their breeding, staging and wintering grounds, have undergone a marked decline in the last decades, and such trends have been more dramatically negative for farmland and insectivorous species (BirdLife International 2004, Sanderson et al. 2006). This can be related to changing conditions both on breeding grounds and on wintering areas.

In Europe, rapid changes in agricultural practices, starting particularly from the second half of 20th century and resulting in intensively cultivated landscape, have caused biodiversity loss and collapse of many farmland bird populations (Donald et al. 2001).

In Africa, the rainfall during the growing, winter, season is fundamental for migrants that stop south of the Sahara, as the precipitations control the vegetation’s growth and therefore the abundance of food, which affects overwinter survival (Ockendon et al. 2013). The level of rainfall in the Sahel area, a major non breeding and staging area for Afro-Palearctic migrants, has turned out to be a key factor, for instance, for the winter survival of the English population of Purple heron *Ardea purpurea* and also Whitethroat *Sylvia communis* (Zwarts et al. 2009).

Vulnerability of populations of migratory birds will also depend on the pattern of movement of the population as a whole, i.e. on whether individuals will spread over different migration routes and wintering quarters or tend to cluster. Studies of 'migratory connectivity', or the extent to which individuals from a given geographical breeding population tend to cluster also during migration and wintering, are at their infancy. The degree of migratory connectivity makes a population more or less susceptible to the risk of environmental stochasticity, or determines negative effects. In the case of high migratory connectivity, birds breeding together stay in the same place during other phases of the annual cycle, and negative events will have severe consequences on the entire population. The opposite will be the case for populations with low migratory connectivity (Marra et al. 2006).

All the above issues about wintering areas, the evolution of migratory strategies, and the causes and mechanisms behind population trends are largely unresolved for virtually all small-size long-distance migratory species. Mainly due to technological limitations, the study of long-distance dispersal and migration of small animals has been impossible to date.

Only in recent years, with the advent of satellite-based position-finders, the tracking of large birds, e.g. storks, gulls and raptors, has become feasible and has led to spectacular insights into their migration patterns and dispersal. This technology, besides the high costs of the tags and satellite use which prevent tracking of a large number of individuals, can be adopted only for large species, owing to the relatively heavy weight of the tags (Wikelski et al 2007). Recently the lightest species that could be tracked by the modern and lighter satellite transmitter (5 grams) is the Cuckoo *Cuculus canorus* (weight about 100 grams) from England, Denmark and Sweden to Africa (cfr. www.bto.org/science/migration/, Willemoes et al. 2014). As a commonly accepted rule, to avoid artefacts and abnormal behaviour, increased energy demands for flying and reduced manoeuvrability, a flying animal should not be equipped with an additional load exceeding 5% of its body mass (Kenward 2001). However, these satellite-based devices are still too heavy to be deployed on small flying animals such as many songbirds.

It is estimated that, only in the Afro-Paleartic system, 2.1 billion birds belonging to thousands of species are moving twice a year across continents (Hahn et al. 2009). However, the vast majority of these birds are small passerines that spend most of the year, up to 8-10 month, away from the breeding grounds (Moreau 1972). Current knowledge of migratory movements, and also of dispersal of these species, is based on ring-recovery data. Even if ringing remains a very powerful and versatile tool to study many different aspects of birds' behaviour and ecology (Spina 1999), only a tiny fraction (<0.001%) of ringed birds is eventually recaptured and provides information on their position at the time of recovery. Moreover, recoveries are not randomly distributed in time and space. In Africa, for instance, the ornithological ringing stations are very few and provide heterogeneous sampling effort; in addition, ringing recoveries do not provide information on routes and time schedules of migration; finally, it is unsuitable to carry out individual-based studies.

Terrestrial radio transmitters allow to follow tagged individuals after fledging, and to get short-range information about dispersal over few weeks over from a hundred metres up to tens of kilometres from the nest of origin (Naef-Daenzer 2007, Naef-Daenzer and Grüebler 2008). Radio-tracking is used widely to explore home ranges, foraging habitats and short range dispersal, but it has seldom been possible to follow individual birds on migration using this technique (Bowlin et al 2005).

Another useful indirect method for obtaining information about migration is the analyses of stable isotopes. The proportions of stable isotopes in tissues reflect the isotopic values of ingested food; changes in certain isotope ratios of an animal's tissues (e.g. feathers) can provide an indication of a change in diet, which is often related to transitions among isotopically distinct habitats (del Rio et al. 2009). Nevertheless, this technique has many limitations, and it is not possible to obtain data on the precise geographic areas where isotopes have been incorporated in the focal tissue (see Hobson & Wassenaar 2008 for a review of stable isotope use).

All these methods, although useful, are largely insufficient to solve all the open questions about bird migration. So far, wintering areas, migrations routes and migration schedule remain largely unknown for the vast majority of small songbirds (Robinson et al 2010).

Recent advances in technology have made it possible to follow the migration of small migratory birds using light level geolocators (Bridge et al. 2011). The geolocators are small and thin (0,5-1 grams) devices, which measure the levels of sunlight in any given date and store the information in an internal memory. Birds are equipped with geolocators in the breeding area, and have to be recaptured for data download after returning from their wintering grounds. Once recovered the devices, sunrise and sunset times can be determined from the recorded light level data for the elapsed time period. Latitude and longitude can then be estimated based on day length and local apparent noon and midnight, respectively, using astronomical equations with a specific software (Lisovski et al. 2012, Lisovski and Hahn 2012).

The precision of positioning on the Earth's surface is quite variable and depends, first, on the period of the year. During the equinoxes, March and September, in fact, day and night have similar length all over the globe, making it impossible to determine position. Particularly for latitude, errors have been documented in the order of 200 km or more (Fudickar et al. 2012, Lisovski et al. 2012). Unfortunately the equinoxes period coincides with the main migration period of many species. Moreover, environmental factors like weather, topography, vegetation, as well as behaviour, are other important factors that influence light intensity and, consequently, the determination of latitude and longitude (Lisovski et al. 2012).

Despite these well-known limitations, geolocators are currently the only tracking devices suitable for tracking small birds (<100 g); their use has increased exponentially, and now represents a widespread way to track migrants on intercontinental scale (Bridge et al. 2011).

However, unlike what happens with satellite-assisted devices, the birds equipped with geolocators must be retrapped one year later to download the information stored in the device. This means that deploying geolocators on philopatric adults is highly preferable over equipping dispersing young, as the former, if they survive, can be retrapped one year later. Geolocators can thus be used only in species with very high philopatric species, without or with minimal breeding dispersal.

In the beginning, the use of these innovative devices to investigate the migratory strategies of birds has largely been limited to relatively large- or medium-sized species, like the barnacle goose *Branta leucopsis* (Eichhorn et al. 2006), the lesser kestrel *Falco naumanni* (Rodrıguez et al. 2009), the European turtle dove *Streptopelia turtur* (Eraud et al. 2013) and many seabirds (Phillips et al. 2007; Guilford et al. 2009; review in Burger and Shaffer 2008).

As the weight and size of geolocators has decreased over time, miniaturized geolocators have been used on smaller birds like waders (Conklin et al. 2010; Minton et al. 2010; Niles et al. 2010; Klaassen et al. 2011), the artic tern *Sterna artica* (Egevang et al. 2010), the hoopoe *Upupa epops* (Bächler et al. 2010), and the red-backed shrike *Lanius collurio* (Tøttrup et al. 2011). In 2009, for the first time, these devices have been used for describing the entire migratory flights of Nearctic-Neotropical migrants, like the purple martin *Progne subis* and the wood thrush *Hylocichla mustelina* (weighing about 50 g), migrating from North to Central and South America (Stutchbury et al. 2009).

Since geolocators are relatively cheap and can give information on a large number of birds, they make individual-based large-scale studies feasible, and can thus potentially provide daily locations and migration trajectories for a number of years: in short, they represent the latest technological advances for those who wish to perform a large-scale study of small migrants. To date, in the last 5 years, many researches have been carried out and many others are now in progress on about 50 different species (reviews in Costantini and Møller 2013).

Thanks to this technology, it has been possible to collect previously unknown information about songbird migration – including the previously unknown wintering quarters of black swift *Cypseloides niger* (Beason et al. 2012) – and connectivity maps of species with large breeding ranges such as the nightingale *Luscinia megarhyncos* (Hahn et al. 2013). Very recently the first evidence has been gathered that Alpine swifts *Tachymarptis melba* can stay airborne for migration, foraging and roosting over a period of more than 6 months. This also raised new questions about how all vital physiological processes, including sleep, can be perpetuated during flight (Liechti et al. 2013). In addition to providing information about the new wintering areas of European Whyneck *Jynk tornquilla* – generally considered to be long-distance Palaearctic-African migrants – the results from tracking individual birds showed that Wrynecks from two Central European populations migrated only relatively short distances to the Iberian Peninsula and northwestern Africa, probably due also to climate changes (Van Wijk et al. 2013). Last but not least, geolocators recently provided the first evidence of the longest fly in small migratory passerines, the northern wheatear *Oenanthe oenanthe*, capable of linking African ecosystems of the Old World with Arctic regions of the New World (Bairlein et al. 2012).

To sum up, geolocators are revolutionizing the study of migration of small passerines, and many exciting discoveries and questions will probably be solved in the near future. We still don't know much about the migration of young – first year – small birds. Following the migration of juvenile individuals by means of geolocators is very difficult because of natal dispersal, whereby juveniles most often breed in a place different from that of origin, making the recovery of tagged birds difficult. In addition, high juvenile mortality (up to 90%, depending on the species) implies that a large number of loggers has to be deployed in order to obtain information on a sufficiently large number of recruits. Hence, in order to study the migration and wintering of juveniles by means of geolocators, the patterns of dispersal of the species under investigation must be known in advance. To date, only one study has been performed on juveniles using loggers, on a medium-sized (around 700 grams) seabird, the Cory's shearwater *Calonectris diomedea* (Péron and Grémillet 2013). This study demonstrated the importance of tracking long-lived species through different life-stages, to fully understand migratory behaviour across age classes and the factors affecting population dynamics, also with conservation implications. So far, no study on this topic has been carried out on small songbirds.

Like the Cory's shearwater, which is endemic of the Mediterranean, others species are currently the focus of ongoing projects, and most of these species are of conservation concern or endangered. Some examples are the aquatic warbler *Acrocephalus paludicola* (Flade et al. 2011, Salewski et al. 2013), the declining purple martin *Progne subis* (Fraser et al. 2012), the lesser kestrel *Falco naumanni* (Rodrıguez et al. 2009), and the critically endangered Balearic Shearwater *Puffinus mauretanicus* (Guilford et al. 2012). A deep knowledge of migration is obviously critical for conservation aims. However, deployment of geolocators may have consequences on individual performance. Thus, evaluating the potentially harmful effects of geolocators deployment is mandatory before embarking in large-scale projects involving large numbers of birds, both for conservation and for ethical reasons (Barron et al. 2010, Vandenabeele et al. 2011, 2012). However, very few studies have actually tested for the effect of geolocators on return rate, reproductive success and, more generally, on life style based on an ad hoc designed experiment with appropriate control groups (Costantini and Møller 2013).

The long-term effects of the deployment of these new instruments have been studied mainly in non-passerines species, like diving and flying seabirds (Quillfeldt et al. 2012), and in one raptor (the lesser kestrel *Falco naumanni*; Rodrıguez et al. 2009). But very few studies provide any information on the effects in small passerines (Costantini and Møller 2013).

The effects of the deployment of these tags may include, first of all, a potentially harmful impact on the return rate of tagged individuals (Stutchbury et al. 2009). In some species, return rates have been smaller than normal, potentially because geolocators increase drag during flight and impinges on aerodynamics (Bowlin et al. 2010). For many species, however, no significant effect on return rate emerged, possibly because of the low statistical power of the tests due to small samples of tagged individuals (Costantini and Møller 2013).

Effects have been demonstrated to occur in morphology between tagged and non-tagged, control birds. For instance, the thin-billed prion *Pachytila belcheri* Quillfeldt et al. (2012) has shown a significant decrease of tail growth in winter, revealing an effect on moult. In the same species, moreover, the geolocator caused physiological change with an increase in hormonal response to stress (Quillfeldt et al. 2012). In another seabird, the Stooty shearwaters *Puffinus griseus,* the tagged individuals showed a lower breeding success and negative effects also in the parental care, and ultimately raised low quality offspring (Adams et al. 2009). In the Artic tern *Sterna paradisaea* geolocator birds exhibited a negative effect of geolocator on clutch size, though the effect was statistically non-significant, probably because of low statistical power of the test. Timing of breeding has been shown to be delayed in the red-backed shrike *Lanius collurio* (Tottrup et al. 2011). In the wheatear *Oenanthe oenanthe,* geolocator birds displayed a lower apparent survival, arrived and started laying eggs on average respectively 3.5 days and 6.3 days later, and had lower breeding success as compared to controls birds.

Summarizing, information from several studies hints at effects of geolocators on phenology, breeding success, morphology of phenotypically plastic traits as well as behaviour. However, no properly designed case-control studies based on large sample sizes ensuring sufficient power to statistical tests have been devised to date. Yet, these are pieces of preliminary information which are crucial to any project on migration which uses these devices, especially with small species with larger device to bird mass ratios. Studies that aim at evaluating the effects that these tags may have on body condition, survival and behaviour, together with the development of new miniaturized loggers, are highly encouraged (Bowlin et al. 2010, Gow et al. 2011, Rodrıguez et al. 2009).

1.2 Natal dispersal

Dispersal is an important key process in ecology and evolution, with major consequences for population dynamics and genetic structure, as well as for species distribution and thus community composition. Movement between a natal site and the site of first breeding is known as natal dispersal and accounts for the largest amount of gene flow and, hence, for the degree of differentiation among populations (Greenwood 1980, Greenwood and Harvey 1982, Clobert et al. 2001). This process consists essentially in 3-steps decisions: decide if emigrating or not from the natal place, moving through an unknown region, and finally settling to breed.

In general, one sex disperses more frequently and/or longer distances than the other; females are the dispersing sex in the majority of birds, while males are the most philopatric sex. Despite the dispersal distances is the main part of long-distance passerines is 3 or 4 orders of magnitude smaller than migration distances, time and energy costs of prospection for suitable sites may be no negligible; more, the dispersers individuals are more likely to incur predation or to lose the advantage of being adapted to local conditions. However, this process also definitely brings benefits to the individuals, and 3 hypotheses have been suggested as ultimate causes shaping the evolution of natal dispersal. The “competition for resources” hypothesis suggests that dispersal by juveniles from their natal area could be derived by reducing competition among kin for limiting resources; the “inbreeding avoidance” hypothesis claims that individuals disperse to avoid the risk of inbreeding with kin (Greenwood 1980). The “competition for mates” hypothesis proposes that individuals disperse to avoid competition for mates; in fact the tertiary sex ratio in most birds is male biased, and individual philopatric males may, thus, have to compete with siblings for limiting mating opportunities. These hypotheses are not mutually exclusive, and risk of inbreeding and competition with kin should result in larger natal dispersal.

These “context-dependent” or “condition-dependent” (Clobert et al. 2009) factors, acting on different scales and stages, have traditionally been identified as fundamental for dispersal decisions in birds; however, few studies have attempted a comprehensive analysis of their effects on dispersal.

Also, differences in natal dispersal are often associated with variation in other traits, because they are ultimately controlled by the same set of genes (Clobert, Le Galliard, Cote, Meylan and Massot, 2009). It has been shown that genes that control melanogenesis in vertebrates pleiotropically influence physiology and behaviour, including boldness and exploration. The covariation between plumage coloration and dispersal has only been investigated, so far, in a single species, the barn owl, *Tyto alba*. Individuals with darker, more pheomelanic plumage disperse over larger distances than less pheomelanic ones (van den Brink, Dreiss and Roulin, 2012; Roulin, 2013). Finally, also parasites may play a major role in generating variation in dispersal strategies, affecting the relative costs of dispersing or being philopatric, because spatial structure of populations can influence the extent of reciprocal adaptation of the host and the parasite.

1.3 Study species: the barn swallow

The barn swallow *Hirundo rustica* is a small - about 20 grams - long-distance migratory passerine, feeding on aerial insects and spending a large proportion of its diurnal life on the wing (Møller 1994, Cramp 1998, Turner 2006).

Sexual dimorphism in size is small, but the length of the tail feathers allows to easily distinguishing between male and female, as adult males have longer tail feathers, which are an important secondary sexual character (Møller et al. 1995). Conversely, the sex of chicks and juveniles is indistinguishable from the morphological characteristics until the first winter, when they undergo complete plumage moult; at this stage the sex can be determined only with molecular techniques, using DNA extracted from small blood samples (Saino et al. 1999, 2008). The adult population has a male-biased tertiary sex ratio (Turner 2006). This farmland bird is semi-colonial and breeds mostly inside rural buildings like farms, cowsheds and stables. In southern Europe, breeding occurs in April-August. Pairs are socially monogamous and they have one to three clutches of 2-7 eggs per season; asynchrony in hatching is small, though not negligible (Møller 1994). Nestlings, which are altricial, hatch about 14 days after the start of incubation; they are fed by both parents and fledge when are about 18-20 days old (Møller 1994). After fledging they may stay at their natal colony for days to weeks before undergoing pre-migratory dispersal, and may also be attended by parents during the post-fledging period. Autumn migration takes place between July and October; European populations winter in equatorial and southern Africa (Turner 2006). Moult of wing and tail feathers occurs once per year mostly in the wintering areas (Ginn and Melville 1983).

Birds arrive to their European breeding quarters by the end of March-May. Adults are extremely philopatric and they return to breed to the same colony, often to the same room and nest where they bred in the previous year (Møller 1994, Turner 2006). Breeding dispersal is well studied in barn swallows. In Switzerland, on 777 swallows ringed as adults to nest, 585 (75%) have returned to nest in the same establishment (Maumary et al. 2007). For a study area in the canton of Ticino recapture rates of adults are 33% for females and 44% for males (Hirschheydt et al. 2006). Similar rates are recorded in Piedmont (Ferro and Boano 1998) and Lombardy (Saino et al 1999). In short, breeding dispersal in this species is very low, while so far no scant information is available about natal dispersal.

Natal dispersal, with male being the most philopatric sex, is common in birds. Estimates of natal dispersal available to date are in the order of 5 km for males and 10 km for females (Turner 2006), but natal dispersal probably varies among geographical populations according to orography and the distribution of suitable breeding sites (Balbontín et al. 2009).

During recent decades, barn swallow populations have been declining in many parts of Europe, and the species is currently classified as SPEC 3, Species of European Conservation Concern (Burfield and van Bommel 2004). Probably factors in both the breeding and wintering areas play a role in population dynamics and contribute to this decline.

In Europe, major changes in agricultural practices have been hypothesized to affect the abundance and reproductive success of many farmland birds like the barn swallow (Møller 2001). Relevant changes consist mainly in the progressive abandonment of traditional cattle sheds in favour of modern and intensive sheds, which are less suitable for swallows (Møller 1994, 2001, Ambrosini et al. 2002, Turner 2006). Indeed the farms with livestock show warmer indoor temperatures, higher insect availabily, presence of hayfields and pastures all around, and this results in an overall larger reproductive success and nestling survival rate, particularly of second broods (Grüebler et al. 2010).

Additional causes of decline can act in the wintering areas and along the migration routes where many others factors may operate, including habitat loss and climate change. There is indirect evidence that stopover and wintering areas are crucial for the conservation of this species (Turner 1994). The ecological conditions in sub-Saharan Africa, as gauged for example by the Normalized Difference Vegetation Index (NDVI), provide information on the amount and vigour of vegetation, and high values can be assumed to reflect favourable environments for wintering birds. These environmental conditions predict arrival and breeding date, as well as breeding success of the barn swallows breeding in Italy, indicating that wintering conditions have major carry-over effects in this species (Saino et al. 2004, Saino et al. 2007).

In addition phenotype, and particularly the length of tail feathers, which is the most important secondary sexual trait currently under directional selection, has also been shown to depend on the ecological conditions in wintering areas during the annual moult, implying that conditions experienced by individuals in Africa can influence the following breeding season and the reproductive success (Møller and Szép 2005, Saino et al. 2004, Saino et al. 2007).

Thus, wintering areas have a key role for barn swallow conservation, and climate changes in Africa may play a negative role in the population dynamics of barn swallows in terms of loss of suitable sites for stopover, decrease in the abundance of insects, etc. (Turner 2009).

Unfortunately, in spite of the thousands of swallows ringed as part of the Project Swallow Euring, the biggest project to have focused on one single species, the wintering areas of swallows remain almost unknown, and only few recoveries are made outside of Europe. The 22 swallows ringed in Switzerland and recovered in Africa were found in Nigeria, Togo, Cameroon, Côte d' Ivoire, Ghana, Central African Republic: this indicates that the main wintering range of the Swiss swallow is located in Central and West Africa (Maumary et al. 2007). Most of Italian recoveries are distributed across Nigeria, Ghana and the Central African Republic (Spina and Volponi 2008).

The barn swallow, for all its features, is an ideal candidate to investigate both migration, by geolocator, and dispersal. The biology and the ecology of this migratory bird is very well-known, and the individuals, adults and chicks in the nest too, can be captured and recaptured with very high efficiency in subsequent years, providing detailed information on breeding dispersal, survival and return rate of adults and juveniles, etc. Nests are easily accessible, and this makes it possible to get detailed information about clutch size and hatching and fledging success of individually marked adults.

Outline of the study

The present study is divided into two parts. The first part (**Chapters 1-2**) focuses on the research on migration of small passerines birds, with miniaturized individual tracking devices - light-level geolocators - specifically used to follow the barn swallow's migration.

The aim of **Chapter 1** was to investigate the migration ecology of three geographical breeding populations of barn swallow in southern Europe (one in Switzerland and two in northern Italy). For this purpose, I equipped adult swallows with geolocators in 2010 and 2011 and, after having recovered and downloaded data in the subsequent years respectively 2011 and 2012, I followed the individuals along their year-round cycle, obtaining their geographic positions during the non-breeding period and their spring and autumn migration routes. I have examined the variance in migration phenology and the distribution residence areas in sub-Saharan Africa in relation to sex, diverse population and different year.

In **Chapter 2**, I have investigated the possible long-term impact of this innovative technology on the productivity, return rate and, more generally, on the life style of the adult swallows, so far one of the smallest species for which this methodology has been used. To achieve this, I tested for differences between birds with and without tag (controls) in the same colonies, while predicting that no difference will be found in productivity and return rates if geolocators do not impact on these traits. I also analysed the possible short-term effect of geolocator applied to parent barn swallows on nestling growth and fledging success of their offspring, because differences in this parameter may indirectly indicate subtle effects of geolocators on adult breeding behaviour during the nestling phase.

Finally, I contributed to the development of this methodology by comparing and optimizing the characteristics of two different model of geolocators' external size and shape (comparing fitness traits but also loss rate), and by developing an optimally-shaped harness for long-term external device attachment, with the purpose of giving a contribution to the evolution of this technique in the study of bird migration.

The second part of the thesis (**Chapters 3-5**) is focused on many different aspects of natal dispersal. With the aim of studying this topic, I have put a huge effort into ringing the largest possible number of barn swallow's nestlings; the probability of finding these recruits the follow year is in fact very small, generally about 5%, due to both mortality and dispersal outside of the study area. At the same time, every year I collected data on many possible factors that can influence the choice of dispersal. In subsequent years, I therefore intensively searched for these recruits, namely the individuals that were recruited as breeding adults in the population in which they hatched. The resulting dataset made possible diversified investigations of this subject.

First of all, in **Chapter 3**, I analysed the natal dispersal propensity (i.e., dispersing or not) and dispersal distance in relation to different factors, with the aim of understanding which are the mechanisms underneath these decisions. Comparing “philopatric” and “dispersing” recruits, respectively individuals that were ringed as nestlings and were recruited as breeding adults in their colony of origin (dispersal distance = 0) and individuals that were recruited in a colony different from that of origin (dispersal distance > 0), I evaluated many possible factors influencing the choice, particularly: the context (colony size and habitat quality represented by the number of livestock at the natal site), the phenotype (body mass relative to siblings indicative of the rank in the brood), the kin (composition of sibling sex in the brood) and the maternal effects (hatching date) of the young.

In **Chapter 4**, I further analysed this theme and I focused in the long-term consequences of family sex composition on breeding success in barn swallows. More in detail, I examined the effect of brood sex composition, obtained by molecular techniques using DNA extracted from small blood samples of nestlings, and brood size that have on morphology and seasonal breeding performance of the offspring that were eventually recruited into the study population as breeding adults.

Finally, in **Chapter 5** I contextualized the natal dispersal also in a genetic contest. Indeed, differences in natal dispersal are often associated with variation in other traits, because they are ultimately controlled by the same set of genes. Then I tested the hypothesis that in the barn swallow the melanic coloration predicts natal dispersal. To archive this, I collected one feather from the white-brownish ventral plumage region for analysis of belly coloration by spectrophotometry. Finally, I also collected data on barn swallow's ectoparasites, particularly haematophagous louse flies *Ornithomya biloba* and chewing lices, because they may play a major role in generating variation in dispersal strategies.

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PART 1

MIGRATION

Chapter 1

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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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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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. Based on the largest dataset of year-round individually tracked adults so far available for any migratory passerine, 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 days in departure dates from and arrival at the breeding sites. Remarkably, the period of residence in sub-Saharan Africa was very similar (157 days) in both 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). 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 an Alpine valley arrived at their breeding colony 7-10 days later than those breeding only 100 km south, in the Po plain. Our study provides entirely novel information on the variance in migration phenology and the distribution residence areas in sub-Saharan Africa in relation to sex, population and year. It supports the usefulness of light-level geolocators as relatively cheap devices for the study of annual routines of large samples of small birds.

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INTRODUCTION

Many migratory bird species that breed in temperate and boreal biomes show long-range latitudinal movements that may lead them to areas located up to several thousands of kilometres from the breeding areas (Alerstam 1990). These movements involve twice a year billions of individuals, mostly songbirds (Hahn et al. 2009). Despite researchers have long been fascinated by such wide-ranging journeys, detailed information on migratory movements has only slowly been accumulating over the decades (Newton 2010). Particularly, data are rare for the smallest-sized species, such as many Palearctic songbirds, migrating over intercontinental distances into sub-Saharan Africa. Individual histories during the non-breeding period are hardly known, due to low efficiency and potential bias inherent in traditional studies based on the recovery of individually ringed birds. New individual tracking systems now available also for relatively small migrants, has circumvented this limitation (Bridge et al. 2013).

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. This has hampered the analysis of the causes and consequences of variation in migratory behaviour among individuals or breeding populations, as well as of the patterns of migratory connectivity of geographical populations. Indeed, population-based data on migration derived by e.g. large-scale bird ringing projects have provided important general information on migration routes and phenology, and on non-breeding distribution (e.g. Rubolini et al. 2002, Ambrosini et al. 2011, Korner-Nievergelt et al. 2014). However, individual-based information is pivotal to our understanding of the evolution of migration. Only 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).

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 (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.

Either sex may experience differential selective pressures during the non-breeding period. For example, males may experience more intense selection for early arrival to the breeding grounds because of the advantages that they can accrue in competition for the best breeding territories and for mating opportunities, including sperm competition (Møller 1994, Rubolini et al. 2004, Spottiswoode and Saino 2010, Morbey et al. 2012). 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, sex specific morphological, physiological and behavioural traits may lead to differences in susceptibility to ecological conditions encountered during the non-breeding period, and thus, 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).

Despite such diverse factors which can generate variation in migration schedules between the sexes, the actual patterns of sex-related variation in phenology and distribution of non-breeding residence areas are only very sparsely known, particularly as far as small migratory birds are concerned.

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 (Rubolini et al. 2007). Recent studies have shown significant migratory connectivity in some species (e.g. (Ambrosini et al. 2009, Gratto-Trevor et al. 2012, Hahn et al. 2013, Trierweiler et al. 2014), implying that individuals breeding in the same geographical region also tend to cluster, at sub-continental scale, during the non-breeding period. Hence, it can be assumed that birds originating from different geographical breeding populations not only show differences in non-breeding ranges but also in the timing of phenological events. 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 altitudinal gradients may produce distinctive clines of variation in breeding phenology, with potential consequences for the other phenological events in the circannual cycle of migratory species.

Inter-annual variation in ecological conditions experienced at any of the stages of the annual life cycle generates 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 (e.g. 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 summary, huge, long-term efforts in the study of bird migration by traditional techniques such as ringing has supplied us with important information on migration phenology and non-breeding distribution of birds. However, technological limits to date have caused a lack of the individual-based information on the non-breeding period of sufficiently large samples of individuals from the same population.

In the present study we aimed at starting to fill this gap of knowledge by equipping with miniaturized individual tracking devices (light-level geolocators) a large number of adults of a small, colonial, trans-Saharan migratory passerine bird, the barn swallow *Hirundo rustica*, from three geographical breeding populations in southern Europe (Switzerland and northern Italy). 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 observed earlier arrival of males before females at the breeding sites (Møller 1994, Møller 2007) is caused by a more northerly area of residence in sub-Saharan Africa and/or a faster pre-breeding migration of males compared to females. However, arrival at and departure from the sub-Saharan residence areas should not differ between sexes (e.g. Saino et al. 2013); 2) due to the harsher climatic conditions 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) the geographic position of the individual sub-Saharan residence area should predict the duration of stay at this site because the farther North a bird stays, the shorter the time it needs for migration, and the longer it can stay at this site; 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: 46°09’ N, 8°55’ E) and two in northern Italy (Piedmont, hereafter SW area, 45°33’ N, 8°44’ E; Lombardy, hereafter SE area, 45°19’N, 9°40’E; Fig. 1). All three areas consist mainly of farmland, dominated by maize and hayfields (see Ambrosini et al. 2012, Scandolara et al. 2013).

Despite being relatively close to each other, differences exist in barn swallow breeding phenology among the three study areas particularly because the N study area is located in an Alpine valley with somewhat lower spring temperature (2 to 3° C) than the SW and SE areas which are located in the Po plain.

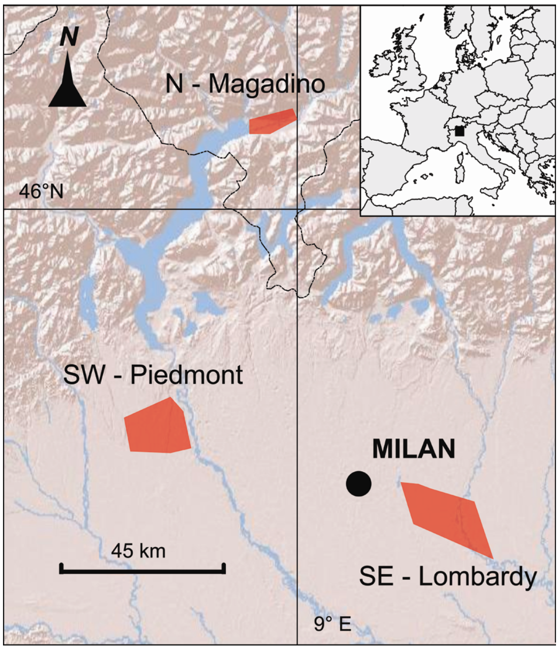

Figure 1. Geographical position of the three study areas (shaded polygons) (N – Magadino, Switzerland; SW – Piedmont, Italy; SE – Lombardy, Italy). The black line shows the border between Italy and Switzerland. Inset: position of the study areas (in black) within Europe.

Geolocator application

In July 2010, we applied 310 SOI-GDL2.10 (Swiss Ornithological Institute) 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 weight of geolocators differed between the two models, being lower for the 2011 model [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 2011 model had also a shorter light stalk (Scandolara et al. in press). 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.)]. 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. in press).

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.

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 et al 2012), the raw positions can be highly inaccurate. We therefore processed the data going through the following steps (details are given in the suppl. material):

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, nest visits were clearly detectable by an abrupt decrease in the light level (suppl. material Fig. 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.

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		
	Males	Females	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 wintering range	62	30	60	32	33	15	44
Duration of stay in the wintering range[a]	49	22	41	30	23	13	35
Departure from the wintering range[a]	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

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

2) We determined sun rise and sun set 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, sun set and sun rise were set automatically by deploying the tailor-made software GeoLocator (Hahn et al. 2013).

3) Within a running window of seven days, we calculated the residuals from a linear regression for 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 sun set and sun rise 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 both events of sunrise and sunset (of the same day or night). This idea is based on the fact that if a bird is stationary, sun rise and sun set 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 sun rise and sun set (±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 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 et al. 2012) from the long stationary periods (>50 days) 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° [s.d.], n = 10). Most likely this difference is due to a slight habitat effect at the roosting sites of the birds. During equinox 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 the equinoxes.

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 analysis of the sub-Saharan residence area we only selected periods with a length of at least 14 days.

For additional details, we refer to the R-code in the suppl. material. 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 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 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 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 stationary periods south of the Sahara longest period;

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 or that it did not affect birds of different sex, breeding population or year of geolocator deployment differentially. We admit that, like in all other studies involving the deployment of tracking devices (independently of their very nature) where by definition the behaviour of untagged birds cannot be monitored, also in the present study this 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 sub-Saharan residence area (covariates). As detailed in the Results section, two-way interaction terms between predictors were included in initial models where relevant and statistically feasible. Although latitude and longitude of the sub-Saharan residence area were positively correlated (either including or excluding the four southernmost-wintering males), their correlation coefficient r was < 0.59, and 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 suppl. material 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, on each sex separately. The residuals were first subjected to a Levene’s test for the homogeneity of variances among the four phenological events within each sex. Levene’s tests were repeated between pairs of phenological events to identify specific differences 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 for significant differences to the real distance between the median locations of the groups. 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, so that the median geographical position of the two years coincided. Thus, we performed the randomisation test on the pooled data from both years while correcting for the year effect. Despite the data were not balanced according to year, sex and population (see Tab 1) which may have reduced the power of the tests, marked differences in SRP between sexes and breeding population would still be detected by this approach. On the other hand, within-year comparisons between sexes and geographical populations would be based on 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

The phenology of the main circannual events (see Fig. 2 for a synopsis) was analysed in linear models with sex, year and population as main effects (Table 2). Date of departure from the breeding colony differed between years and sexes but not among study areas. In 2010 departure occurred 5 days later than in 2011. Independently of any year effect, females deserted their breeding colony 3 days earlier than males.

Duration of post-breeding migration was also significantly different between years, being 10 days shorter in 2010 than in 2011 (Fig. 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 (Fig. 2).

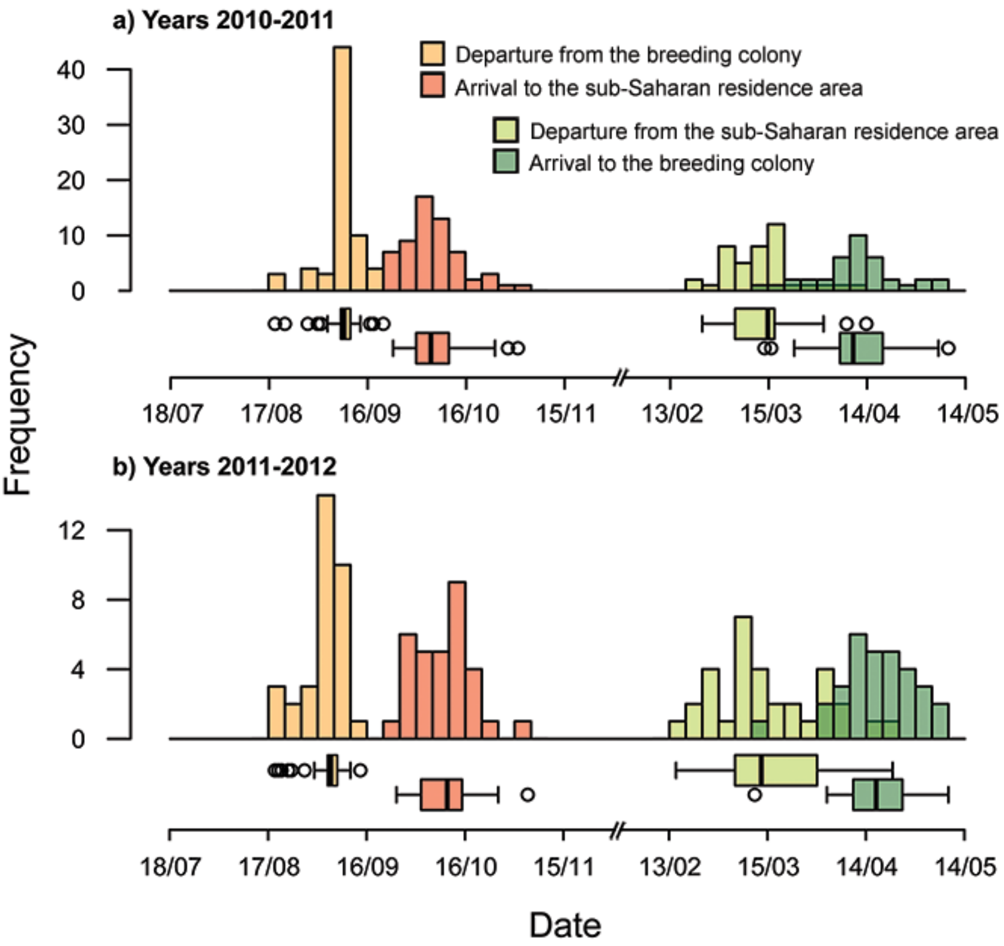

Figure 2. Phenology of autumn and spring migration of barn swallows tracked with geolocators. Upper graph shows timing of autumn migration for the two study years. Lower graph shows timing for spring migration for the two study years. Boxplots show median (black line), 25% and 75% quantile (box), 90%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

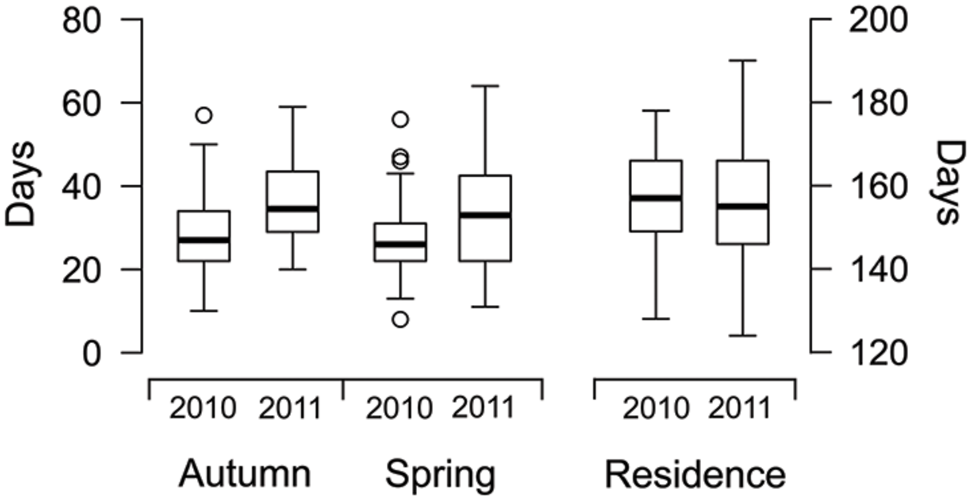

Figure 3. Boxplot of median duration of post- and pre-breeding migration (left) and of duration of stay in the sub-Saharan residence area (right) (box: interquartile range; whiskers: extreme values except dots, which are the values >1.5 times the interquartile range). Year values (2010 and 2011) refer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

	F	df	P	Least-square means		
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)**

Superscript “a” indicates significant ($P < 0.05$) pairwise difference at post-hoc tests

Table 3. Effects (s.e.) 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 four males staying in southern Africa are shown. Bolded terms are statistically significant at: *: $P < 0.05$; **: $P < 0.01$.

	Duration of stay (n = 71/66)	Departure (n = 73/68)	Duration of migration (n = 68/63)	Arrival date (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 SRP 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)***

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 (Tab. 2). Duration of pre-breeding migration was significantly shorter (7 days) for birds tagged in 2010 than in 2011 (Fig. 3) and arrival to the breeding areas was consequently earlier (9 days). In addition, arrival date was significantly later, by 7-10 days, 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 days earlier than those of females (Tab. 2).

In addition, we tested for differences in the variance among departure and arrival events. The variance differed significantly among the four phenological events for males (Levene's test; $F_{3,220} = 12.73$, $P < 0.001$), 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. For males variance increased significantly 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. For females variances for the first two events did not differ, but was significantly smaller than for the following two events (for statistics see suppl. material). 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 $P > 0.4$).

Spatial distribution of individual sub-Saharan residence positions

For 92 tracks we could calculate a sub-Saharan residence position (Fig. 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 stayed more to the west, in Mali and Senegal (1 male, 1 female), while five SRP of males were located in southern Africa, with their centres south of 19°S. No female moved further south than 1°S.

There was a statistically significant difference in the sub-Saharan residence areas between the two years of the study. Median location of the 59 individuals in 2011 was (7.0°N, 12.8°E) and of the 33 individuals in 2012 it was (3.2°N, 15.3°E). The median location in 2012 was 506 km further to the SE than in 2011. When assigning the year randomly to the individuals repeatedly (4999 times), the distance between the median positions was 139 km.

The observed distance of the median location between the years (506 km) was significantly higher than expected by chance ($P = 0.002$). 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. Based on the randomization test, there were no statistically significant differences in the spatial distribution of sexes or breeding populations (all pairwise >0.06, see suppl. material).

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 days (suppl. material Fig. A1). Median distance between the positions of these 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. There was no directional preference for the individual displacements between the non-breeding stationary periods (Rayleigh-test $r = 0.04$, $n = 22$, $P > 0.90$).

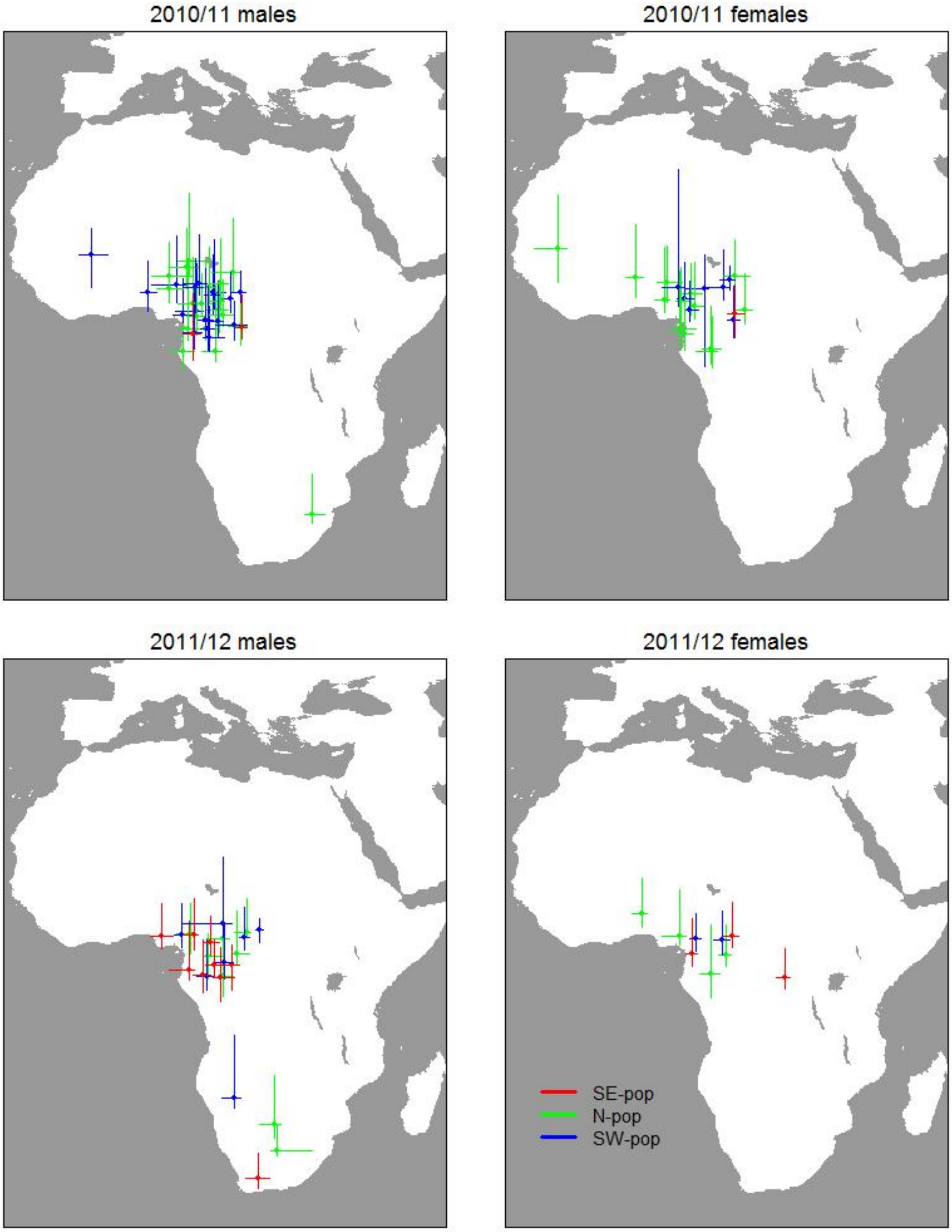

Figure 4. Spatial distribution of the individual sub-Saharan residence positions for all individuals (N = 94 tracks). In case of more than one stationary period south of the Sahara only the longest period is represented. The centre of the density distribution and the 90% range in longitude and latitude (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.

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

We tested whether the SRP affected the phenology 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'; Tab. 3). Duration of stay and departure from SRP were unaffected by latitude or longitude in the whole dataset (Tab. 3), but latitude and longitude effects emerged in the reduced dataset (Tab. 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 (Tab. 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 (Tab. 3). Arrival date to the breeding colonies was instead strongly and consistently predicted by latitude and longitude of the SRP in both datasets (Tab. 3). Birds from more northern and eastern locations arrived earlier (Tab. 3, Fig. 5) than those from further south and west. Finally, latitude of the SRP did not differentially predict the phenology of non-breeding events of either sex (details see suppl. Material).

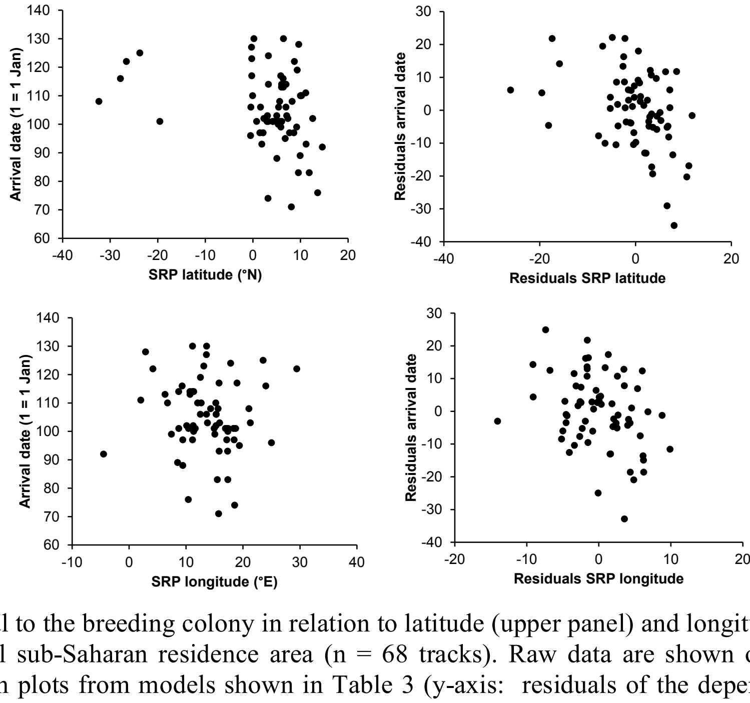

Figure 5. Arrival to the breeding colony in relation to latitude (upper panel) and longitude (lower panel) of the individual sub-Saharan residence area (n = 68 tracks). Raw data are shown on the left, while partial regression plots from models shown in Table 3 (y-axis: residuals of the dependent variable on all of the other predictors in the model; x-axis: residuals of the regression of a given predictor on all of the other predictors) are shown on the right panel.

DISCUSSION

This is the first study presenting a sample of individual based tracks large enough to investigate population and sex specific variation in the phenology of the non-breeding period. We used miniaturized light-level geolocators to obtain individual-based information on the phenology of post- and pre-breeding migration and the duration and position of the sub-Saharan residence area.

Phenology of non-breeding period events

Surprisingly, there was only a 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, Møller 2007). At least, there was a non-significant difference in the mean of the arrival dates in line with the expected trend. We found the same non-significant trend between the sexes, when analysing the recapture dates instead the logger data of these individuals. While the difference in arrival dates was not statistically significant, it is consistent with a statistically significant protandry of 3 days inferred from a large sample of first capture dates at the breeding colonies of two or more years old individuals (Saino et al. 2004b). Thus, we 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. Alternatively, females may require reaching pre-migratory fattening areas earlier than males, because of their investment in the eggs of up to three clutches per breeding seasons.

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 days, respectively, in the three years encompassed by this study. 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 significant differences in phenology were observed among populations. A close inspection to the model-estimated values of the 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 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 lifecycle, but rather results from 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 significant differences 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 days), shorter post-breeding migration period (10 days), earlier arrival at the sub-Saharan residence area (5 days), shorter pre-breeding migration (7 days) and earlier arrival to the breeding colony (9 days) 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 (Fig. 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 8th and 12 to 13th September. Peak departure was on the 7th, and by the 13th 90% of the tracked birds had left their breeding sites. In 2011 heavy rain was recorded on the 4 to 5th September. 60% of the tracked individuals left between 3rd to 6th September, and by the 10th, before the next heavy rainfall (on the 11th), 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. 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 days (Jenni and Winkler 1994) while the duration of stay at the sub-Saharan residence area we observed was 157 days in both years, suggesting that moult *per se* is unlikely to constrain the onset of migration. However, 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.

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

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 seemed to be fairly resident during wintering: even those that were found to have more than one African residence area (see Methods) stayed within a region which is relatively small for a highly vagile species which can travel hundreds of kilometres per day on foraging trips (NS, unpubl. data).

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. 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 in Italy during the breeding season over approximately one century (Saino et al. 2004a, Spina and Volponi 2008) and confirms the migratory connection of barn swallows between Italy (and presumably southern Switzerland) and mainly western equatorial Africa.

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.

Males and females appeared to broadly overlap in the phenology of migration and sub-Saharan residence positions, and also between populations there was no noticeable difference. In the first study year (2010/11) the tracked birds occupied residence areas in sub-Saharan Africa further north than in the second study year (2011/12). They left their residence areas a bit earlier (not significantly) and arrived earlier in the breeding colonies (Tab. 2). This is in line with the result that regardless of the year effect birds staying further north arrived earlier at the breeding colonies (Tab. 3). Thus, we can conclude that early arrivals at the breeding colonies are birds with sub-Saharan residence areas further north and east than those of late arrivals. The analyses carried out on the reduced dataset, excluding the five SRP 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 for 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 can accrue both viability advantages during migration but also natural and sexual selection advantages at the breeding grounds in terms of access to the best, early arriving mates, sperm competition and also number of reproductive events per season (see Introduction for references). Hence, the present findings suggest positive selection for spending the non-breeding period closer to the breeding range, though selection on males should be stronger in a protandrous species, with inter-sexual selection by choosy females also via sperm competition, and with male-biased tertiary sex ratio. However, we must consider that distance is only one part of the story. There was no 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. In the first study year, mean April (2011) temperatures in the western Mediterranean (where most of our geolocator birds migrated through, based on longitudinal positions during spring migration) and in the breeding areas were extraordinarily high, with up to 4°C above the long-term average (IRI/LDEO Climate Data Library 2014; suppl. material Fig. A2). 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, we assume that 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 for 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.

In conclusion, we have explored sex- and year-dependent variation in non-breeding phenology and distribution of barn swallows from three geographical populations breeding under partly different ecological conditions. We used the largest dataset of year-round individually tracked adults so far available for any migratory passerine. The distribution of the sub-Saharan residence areas we recorded is consistent with the available information from ring recoveries, which however required one century to be accumulated. We uncovered variation in migration decisions as well as in the distribution of residence areas and phenology according to all the main factors that were at the focus of our study. We disclosed clear and partly unexpected effects of the position of the sub-Saharan residence areas, its duration of stay and departure from there. Most importantly 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 ranges. The present study corroborates the utility of light-level geolocators for the study of migration of small birds, under the assumption that deployment of these devices does not markedly affect their migration behaviour.

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SUPPLEMENTARY MATERIAL

M1: R-code for the data analysis of light-level geolocators

```
# Analysis of light-level logger data for SOI-GDL2.10 & SOI-GDL2.11
# by F. Korner-Nievergelt & F. Liechti
# August 2013
# R 3.0.0 (2013-04-03)
#--------------------------------------------------------------------------------------------------
# contents (every part can be run in its own)
# 0) libraries and functions
# 1) data input and
# 2) definition of weights for each sun-event according to the running-maximum-method
#    point (3 and 4) in description of methods
# 3) identify stationary periods using change-point for events with weight > 0
#     point (5 and 6) in description of methods
# 4) merging of stationary periods according to overlap of the kernels
#     point (7) in description of methods
#
#--------------------------------------------------------------------------------------------------
# 0) libraries and functions
#--------------------------------------------------------------------------------------------------
#
# load packages
library(ks)
library(birdring)
library(geosphere)
#--------------------------------------------------------------------------------------------------
# own functions
ownmode <- function(x, w=NULL) {
# mode of x
# x: vector of numerics
# w: vector of plain (!) numbers of weights   -> does not work yet...
if(is.null(w)){
 if(sum(!is.na(x))>1){
 x <- x[!is.na(x)]
 xdens <- density(x)
 xmax <- xdens$x[xdens$y==max(xdens$y, na.rm=TRUE)]
 }
 if(sum(!is.na(x))<2) xmax <- NA
 }
if(!is.null(w)){
 x <- rep(x,w)
 if(sum(!is.na(x))>1){
 x <- x[!is.na(x)]
 xdens <- density(x)
 xmax <- xdens$x[xdens$y==max(xdens$y, na.rm=TRUE)]
 }
 if(sum(!is.na(x))<2) xmax <- NA
 }
 return(mean(xmax))
 }

insidekernel <- function(x,y, kernelobj, percentage=95){
# looks up whether a point (x,y) is inside a specific kernel density isoline
		kritdensity <- contourLevels(kernelobj, prob=1-percentage/100)
		densitymat <- matrix(kernelobj$estimate, ncol=length(kernelobj$eval.points[[1]]), nrow=length(kernelobj$eval.points[[2]]),
byrow=FALSE)
		nearestx <- kernelobj$eval.points[[1]][abs(kernelobj$eval.points[[1]]-x)==min(abs(kernelobj$eval.points[[1]]-x))][1]
		nearesty <- kernelobj$eval.points[[2]][abs(kernelobj$eval.points[[2]]-y)==min(abs(kernelobj$eval.points[[2]]-y))][1]
		insidek <- densitymat[kernelobj$eval.points[[1]]==nearestx, kernelobj$eval.points[[2]]==nearesty]>=kritdensity
		return(insidek)
		}
#--------------------------------------------------------------------------------------------------
# set working directory
setwd("R:/Auswertungen/Geolocator/BarnSwallow/data/") # vowa
#setwd("D:/Dropbox/Vogelwarte/felix/schwalben")
#
#--------------------------------------------------------------------------------
# 1)  data input
#--------------------------------------------------------------------------------
#
# read data the four data sets
dat1 <- read.table("positions2-8 _CH2010.csv", sep=";", header=TRUE)
```

```
dat2 <- read.table("positions2-8 _IT2010.csv", sep=";", header=TRUE)
dat3 <- read.table("positions2-8 _CH2011.csv", sep=";", header=TRUE)
dat4 <- read.table("positions2-8 _IT2011.csv", sep=";", header=TRUE)
nrow(dat1)+nrow(dat2)+nrow(dat3)+nrow(dat4)
# merging the data sets
dat <- merge(dat1,dat2,all=T)
dat <- merge(dat,dat3,all=T)
dat <- merge(dat,dat4,all=T)
#
#-------------------------------------------------------------------------------------
# 2)  definition of weights for each sun-event according to the running-maximum-method
#-------------------------------------------------------------------------------------
#
# define various date variables
dat$tFirst.date <- strptime(as.character(dat$tFirst), format="%Y-%m-%d %H:%M")
dat$tSecond.date <- strptime(as.character(dat$tSecond), format="%Y-%m-%d %H:%M")
dat$month <- as.numeric(substring(as.character(dat$tFirst.date), 6, 7))
dat$dayofyear <- dat$tFirst.date$yday+1
dat$dayofwinter <- dat$dayofyear
dat$year <- dat$tFirst.date$year+1900
dat$dayofwinter[dat$dayofyear<180] <-dat$dayofyear[dat$dayofyear<180]+ ifelse(dat$year[dat$dayofyear<180]==2012, 366, 365)
dat <- dat[order(dat$logCode, dat$tFirst.date),]
dat <- dat[dat[,2]!="",]
# max daylenght and min nightlength for an 2m sized window
daylength <- vector(mode="numeric", length(dat$tFirst.date))
nightlength <- vector(mode="numeric", length(dat$tFirst.date))
daylength <- ifelse (dat$type == 1, difftime(dat$tSecond.date,dat$tFirst.date,units="mins"), 0)
nightlength <- ifelse (dat$type == 2, difftime(dat$tSecond.date,dat$tFirst.date,units="mins"), 10000)
maxday <- vector(mode="logical",length(daylength))
minnight <- vector(mode="logical",length(daylength))
# calculation of the weight factor based on day/nightlenght
# weight acounts for how many times a specific day/nightlength is the least shaded one within the moving window of size m
dt <- vector(mode="numeric",length(daylength))      # mean difference
w1 <- vector(mode="numeric",length(daylength))      # weight factor
dtdet <- vector(mode="numeric",length(daylength))   # mean detrended difference
w1det <- vector(mode="numeric",length(daylength))   # weight factor detrended
n_w1 <- vector(mode="numeric",length(daylength))
m <- 3 # size of moving window "+-m"
i <- 2*m+1
j <-  -2*m
for (i in (2*m+1):(length(daylength)-2*m)) {
  for (j in seq(-2*m,2*m,by=2))  {
    if (dat$logCode[i-2*m]==dat$logCode[i+2*m])  {
      if (dat$type[i+j] == 1) {
        mod <- lm(daylength[seq((i-2*m),(i+2*m), by=2)]~dat$dayofwinter[seq((i-2*m),(i+2*m), by=2)])
        residdaylength <- resid(mod)
        dtdet[i+j] <-  max(residdaylength)-residdaylength[j/2+m+1]
        w1det[i+j] <- w1det[i+j] + dtdet[i+j]

        dt[i+j] <-  max(daylength[(i-2*m):(i+2*m)])-daylength[i+j]
        w1[i+j] <- w1[i+j] +dt[i+j]
        n_w1[i+j] <- n_w1[i+j] + 1
      }
      if (dat$type[i+j] ==2) {
        mod <- lm(nightlength[seq((i-2*m),(i+2*m), by=2)]~dat$dayofwinter[seq((i-2*m),(i+2*m), by=2)])
        residnightlength <- resid(mod)
        dtdet[i+j] <- residnightlength[j/2+m+1] - min(residnightlength)
        w1det[i+j] <- w1det[i+j] + dtdet[i+j]

        dt[i+j] <- nightlength[i+j] - min(nightlength[(i-2*m):(i+2*m)])
        w1[i+j] <- w1[i+j] + dt[i+j]
        n_w1[i+j] <- n_w1[i+j] + 1
      }
    }}
}
# calculating weights
w1 <- w1/(n_w1)
w1det <- w1det/(n_w1)
c1 <- 5      # level1
c2 <- 10     # level2
c3 <- 20     # level3
w2 <- 0
w2 <- ifelse (w1 < c3, 1, 0)
w2 <- ifelse (w1 < c2, 2, w2)
w2 <- ifelse (w1 < c1, 3, w2)
w2det <- 0
```

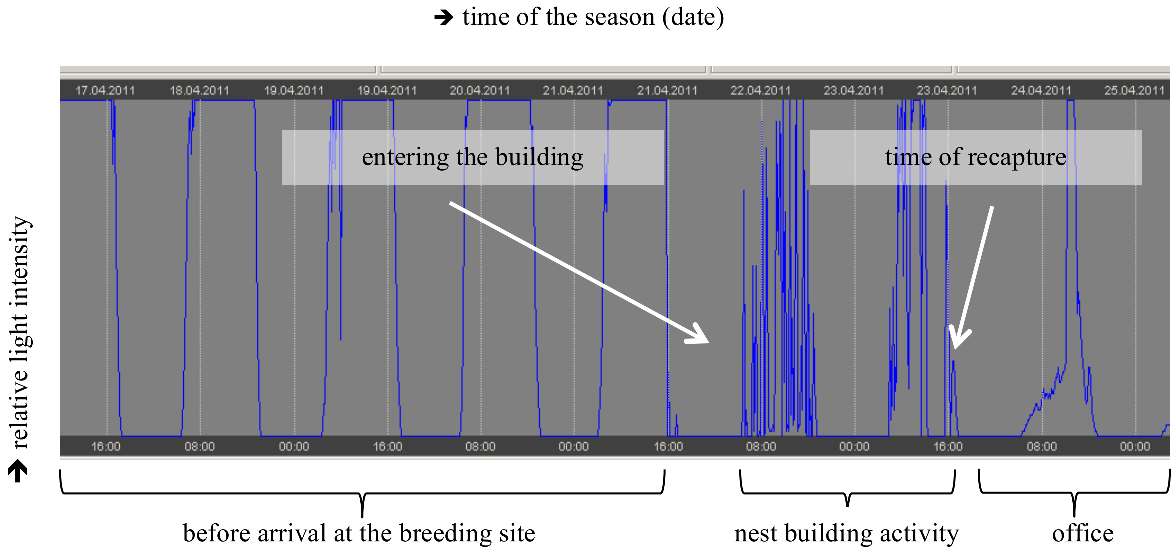
```
w2det <- ifelse (w1det < c3, 1, 0)
w2det <- ifelse (w1det < c2, 2, w2det)
w2det <- ifelse (w1det < c1, 3, w2det)
dat$daylength <- ifelse(dat$type==1,daylength,nightlength)
dat$mean_td <- w1
dat$posweight <- w2
dat$mean_tddet <- w1det
dat$posweightdet <- w2det
# delete dates from 13. 9. to 3. 10. and from 10.3. to 30.3. due to equinox
dat$equinox <- (dat$dayofyear >= 256 & dat$dayofyear <= 276)| (dat$dayofyear>=69 & dat$dayofyear<= 89)
#dat$equinox <-(dat$dayofyear >= 245 & dat$dayofyear <= 287)| (dat$dayofyear>=58 & dat$dayofyear<= 100) # plusminus 21 days
write.table(dat, file="../data/positions2_8_weight_1-1-20_max2unddet.txt", row.names=FALSE, sep="\t")
#
#------------------------------------------------------------------------------------------------------------
# 3)  identify stationary periods using change-point for events with weight > 0
#------------------------------------------------------------------------------------------------------------
#
dat <- read.table("R:/Auswertungen/Geolocator/BarnSwallow/data/positions2_8_weight_1-1-20_max2unddet.txt", header=TRUE, sep="\t")
dat$tFirst.date <- strptime(as.character(dat$tFirst), format="%Y-%m-%d %H:%M")
dat$tSecond.date <- strptime(as.character(dat$tSecond), format="%Y-%m-%d %H:%M")
plot(dat$mean_tddet~dat$posweightdet, ylim=c(0,50))
datw <- dat[dat$posweightdet>0,]    # select only events with detrended weight >0
#datw <- dat[dat$posweight>0,]     # select only events with weight >0
#parameters for regression method
ndays <- 7
tsds <- 0.1 # threshold difference in slope (to identify diffbetas close to zero)   POSWEIGHT DET
tsds2 <- 0.04 # threshold difference in slope (for the sum of two consecutive diffbetas)   POSWEIGHT DET
trsh2 <-  0.05 # threshold slope for sun events~date, higher=movement
tslon <- 0.2  # threshold slope for longitude within a phase
# going through all loggers
for(i in 1:nlevels(dat$logCode)){
  log_code <-  levels(dat$logCode)[i]
  tab <- datw[datw$logCode==log_code,]
  datrise <- tab[tab$type==1,]
  datset <- tab[tab$type==2,]
  datrise$hour <- as.numeric(substring(as.character(datrise$tFirst.date), 12, 13))
  datrise$min <- as.numeric(substring(as.character(datrise$tFirst.date), 15, 16))
  datrise$hour.dec <- datrise$hour + datrise$min/60
  datrise$date.num <- as.numeric(datrise$tFirst.date)/60/60/24
  datset$hour <- as.numeric(substring(as.character(datset$tFirst.date), 12, 13))
  datset$min <- as.numeric(substring(as.character(datset$tFirst.date), 15, 16))
  datset$hour.dec <- datset$hour + datset$min/60
  datset$date.num <- as.numeric(datset$tFirst.date)/60/60/24
  # caclulation oft the lin.regr. event-time~datum for ndays before and ndays after, separately for sunset and sunrise
  tab$beta.past <- NA
  tab$beta.future <- NA
  tab$R2.past <- NA
  tab$R2.future <- NA
  tab$density.past <- NA
  tab$density.future <- NA
  tab$resid.past <- NA
  tab$resid.future <- NA
  tab$p.past <- NA
  tab$p.future <- NA
  tab$date.num <- as.numeric(tab$tFirst.date)/60/60/24
  for(k in 1:nrow(tab)){
    if(tab$type[k]==1) tempdat <- datrise else tempdat <- datset
    index <- tempdat$tFirst.date == tab$tFirst.date[k]
    tempdat$rownumber <- 1:nrow(tempdat)
    # regressions in past
    indexpast <- tempdat$rownumber >= (tempdat$rownumber[index]-ndays) & tempdat$rownumber < tempdat$rownumber[index]
    if(sum(indexpast)>2){
      mod <- lm(hour.dec~date.num, data=tempdat[indexpast,])
      tab$beta.past[k] <-  coef(mod)[2]
      tab$R2.past[k] <- summary(mod)$r.squared
      tab$density.past[k] <- dnorm(tempdat$hour.dec[index], mean=predict(mod, newdata=tempdat[index,]), sd=summary(mod)$sigma)
      plower <- pnorm(tempdat$hour.dec[index], mean=predict(mod, newdata=tempdat[index,]), sd=summary(mod)$sigma)
      if(plower>0.5) plower <- 1-plower
      tab$p.past[k] <- 2*plower
      tab$resid.past[k] <- tempdat$hour.dec[index]- predict(mod, newdata=tempdat[index,])
    }
    # regressions in future
    indexfuture <- tempdat$rownumber > tempdat$rownumber[index] & tempdat$rownumber <= (tempdat$rownumber[index]+ndays)
    if(sum(indexfuture)>2){
      mod <- lm(hour.dec~date.num, data=tempdat[indexfuture,])
      tab$beta.future[k] <-  coef(mod)[2]
```

```
      tab$R2.future[k] <- summary(mod)$r.squared
      tab$density.future[k] <- dnorm(tempdat$hour.dec[index], mean=predict(mod, newdata=tempdat[index,]), sd=summary(mod)$sigma)
      plower <- pnorm(tempdat$hour.dec[index], mean=predict(mod, newdata=tempdat[index,]), sd=summary(mod)$sigma)
      if(plower>0.5) plower <- 1-plower
      tab$p.future[k] <- 2*plower
      tab$resid.future[k] <- tempdat$hour.dec[index]- predict(mod, newdata=tempdat[index,])
    }
  }   # k
  matchindex <- match(dat$tFirst.date[dat$logCode==log_code], tab$tFirst.date)
  dat$p.past[dat$logCode==log_code] <- tab$p.past[matchindex]
  dat$resid.past[dat$logCode==log_code] <- tab$resid.past[matchindex]
  dat$beta.past[dat$logCode==log_code] <- tab$beta.past[matchindex]
  dat$R2.past[dat$logCode==log_code] <- tab$R2.past[matchindex]
  dat$density.past[dat$logCode==log_code] <- tab$density.past[matchindex]
  dat$p.future[dat$logCode==log_code] <- tab$p.future[matchindex]
  dat$resid.future[dat$logCode==log_code] <- tab$resid.future[matchindex]
  dat$beta.future[dat$logCode==log_code] <- tab$beta.future[matchindex]
  dat$R2.future[dat$logCode==log_code] <- tab$R2.future[matchindex]
  dat$density.future[dat$logCode==log_code] <- tab$density.future[matchindex]
  tab$diffbeta <- tab$beta.future-tab$beta.past
  tab$cpboth <- NA
  for(k in 2:(nrow(tab)-2)){
    if((tab$dayofyear[k]- tab$dayofyear[k-1])<2){
      tab$cpboth[k] <- abs(tab$diffbeta[k]+tab$diffbeta[k-1])>2*tsds2
    }
  }
  tab$cpboth[is.na(tab$cpboth)] <- FALSE
  #  find changepoints and decide whether phases are stationary or not
    datrise <- tab[tab$type==1,]    # redefine these data sets, now including diffbetas
  datset <- tab[tab$type==2,]
  datrise$hour <- as.numeric(substring(as.character(datrise$tFirst.date), 12, 13))
  datrise$min <- as.numeric(substring(as.character(datrise$tFirst.date), 15, 16))
  datrise$hour.dec <- datrise$hour + datrise$min/60
  datrise$date.num <- as.numeric(datrise$tFirst.date)/60/60/24
  datset$hour <- as.numeric(substring(as.character(datset$tFirst.date), 12, 13))
  datset$min <- as.numeric(substring(as.character(datset$tFirst.date), 15, 16))
  datset$hour.dec <- datset$hour + datset$min/60
  datset$date.num <- as.numeric(datset$tFirst.date)/60/60/24
  datfulli <- data.frame(dayofyear=c(200:365, 1:180))
  datfulli$phase <- 1
  datfulli$nevents <- 0
  datfulli$nevens[1] <- NA
  datfulli$stationary <- NA
  datfulli$cp <- FALSE
  for(k in 2:nrow(datfulli)){
    datfulli$nevents[k] <- sum(is.element(tab$dayofyear, datfulli$dayofyear[k]))
    if(datfulli$nevents[k] ==0) datfulli$phase[k] <- datfulli$phase[k-1]
    if(datfulli$nevents[k] ==0) next
    # for rise
    askifstationaryrise <- NA
    askifcprise <- FALSE
    if(is.element(datfulli$dayofyear[k], datrise$dayofyear)){
      krise <- c(1:nrow(datrise))[datrise$dayofyear==datfulli$dayofyear[k]]
      askifstationaryrise <- abs(datrise$diffbeta[krise]) < tsds  & mean(c(abs(datrise$beta.past[krise]), abs(datrise$beta.future[krise])),
na.rm=TRUE) < trsh2 & !datrise$cpboth[krise]
      if(!is.na(askifstationaryrise)){
        if(!askifstationaryrise){
          diffdiffbeta1 <-  datrise$diffbeta[krise] -datrise$diffbeta[krise-1]
          diffdiffbeta2 <-  datrise$diffbeta[krise+1] -datrise$diffbeta[krise]
          if(length(diffdiffbeta1)>0&length(diffdiffbeta2)>0) askifcprise <- sign(diffdiffbeta1) != sign(diffdiffbeta2)
        }}
    }# for rise
    # for set
    askifstationaryset <- NA
    askifcpset <- FALSE
    if(is.element(datfulli$dayofyear[k], datset$dayofyear)){
      kset <- c(1:nrow(datset))[datset$dayofyear==datfulli$dayofyear[k]]
      askifstationaryset <- abs(datset$diffbeta[kset]) < tsds  & mean(c(abs(datset$beta.past[kset]), abs(datset$beta.future[kset])),
na.rm=TRUE) < trsh2 & !datset$cpboth[kset]
      if(!is.na(askifstationaryset)){
        if(!askifstationaryset){
          diffdiffbeta1 <-  datset$diffbeta[kset] - datset$diffbeta[kset-1]
          diffdiffbeta2 <-  datset$diffbeta[kset+1] -datset$diffbeta[kset]
          if(length(diffdiffbeta1)>0&length(diffdiffbeta2)>0) askifcpset <- sign(diffdiffbeta1) != sign(diffdiffbeta2)
        }}
    }# for set
```

```
    # decide both on rise and set  (both need to be stationary but NAs are ignored)
    if(sum(c(askifstationaryrise,askifstationaryset), na.rm=TRUE)==sum(!is.na(c(askifstationaryrise,askifstationaryset))))
datfulli$stationary[k] <- TRUE
    # non stationary if at least one is FALSE
    if(!is.na(askifstationaryrise))  if(!askifstationaryrise)   datfulli$stationary[k] <- FALSE
    if(!is.na(askifstationaryset))  if(!askifstationaryset)   datfulli$stationary[k] <- FALSE
    if(is.na(askifstationaryrise) &  is.na(askifstationaryset))  datfulli$stationary[k] <- NA

    if(!is.na(askifcpset)&!is.na(askifcprise)){
      if(askifcpset|askifcprise) datfulli$cp[k] <- TRUE
      if(askifcpset|askifcprise) datfulli$phase[k] <- datfulli$phase[k-1] +1
      else  datfulli$phase[k] <- datfulli$phase[k-1]
    }
    if(!is.na(askifcpset)&is.na(askifcprise)){
      if(askifcpset) datfulli$cp[k] <- TRUE
      if(askifcpset) datfulli$phase[k] <- datfulli$phase[k-1] +1
      else  datfulli$phase[k] <- datfulli$phase[k-1]
    }
    if(is.na(askifcpset)&!is.na(askifcprise)){
      if(askifcprise) datfulli$cp[k] <- TRUE
      if(askifcprise) datfulli$phase[k] <- datfulli$phase[k-1] +1
      else  datfulli$phase[k] <- datfulli$phase[k-1]
    }
    if(is.na(askifcpset)&is.na(askifcprise)){
      datfulli$phase[k] <- datfulli$phase[k-1]
    }
  } # close k  (rows of datfulli)
  tab$phase <- datfulli$phase[match(tab$dayofyear, datfulli$dayofyear)]
  tab$stationary <- datfulli$stationary[match(tab$dayofyear, datfulli$dayofyear)]
  tab$cp <- datfulli$cp[match(tab$dayofyear, datfulli$dayofyear)]
  dat$phase[dat$logCode==log_code] <- tab$phase[matchindex]
  dat$stationary[dat$logCode==log_code] <- tab$stationary[matchindex]
  dat$cp[dat$logCode==log_code] <- tab$cp[matchindex]
  dat$cpboth[dat$logCode==log_code] <- tab$cpboth[matchindex]
  # fill up the phases and decide for stationary or not in the non-weighted data set
  phasen <- unique(dat$phase[dat$logCode==log_code])
  phasen <- phasen[!is.na(phasen)] # delete NAs
  dat$slopelon <- NA
  dat$slopelat <- NA
  datw$phase <- NA
  for(p in phasen){
    index <- dat$logCode==log_code & dat$phase==p
    index[is.na(index)] <- FALSE
    firstday <- min(dat$dayofwinter[index])
    lastday <-  max(dat$dayofwinter[index])
    index2 <-  dat$logCode==log_code & dat$dayofwinter>=firstday & dat$dayofwinter<=lastday
    dat$phase[index2] <- p
    statav <- ifelse(mean(dat$stationary[index2], na.rm=TRUE)<0.5, FALSE, TRUE)
    dat$stationary[index2] <- statav
    # add slope for longitude and latitude based on weighted positions
    datw$phase[datw$dayofwinter>=firstday & datw$dayofwinter<=lastday & datw$logCode==log_code] <- p
    indexw <- datw$logCode==log_code & datw$phase==p
    indexw[is.na(indexw)] <- FALSE
    if(sum(indexw)>1){
      slopelon <- coef(lm(lon~dayofwinter, datw[indexw,]))[2]
      if(sum(indexw)-sum(is.na(datw$lat[indexw]))>1)
        slopelat <- coef(lm(lat~dayofwinter, datw[indexw,]))[2]
      dat$slopelon[index2] <- slopelon
      dat$slopelat[index2] <- slopelat
    }
  }# close p
  dat$stationary[dat$logCode==log_code]<- abs(dat$slopelon[dat$logCode==log_code])< tslon

  tab <- dat[dat$logCode==log_code,]
  tab$diffbeta <- tab$beta.future-tab$beta.past
  # draw cp_regression graph
  jpeg(file.path("R:/Auswertungen/Geolocator/BarnSwallow/temp", paste0("regr", log_code, "tsdiff", tsds, "tsboth", tsds2, "tsslope", trsh2,
"days", ndays, "tslon", tslon ,"det.jpg")), width = 480, height = 550)
  par(mfrow=c(4,1), mar=c(2,4,1,1))
  plot(datrise$tFirst.date, datrise$hour.dec, type="l", main=log_code, col="orange", xlim=as.numeric(range(tab$tFirst.date)), ylab="time")
  abline(v=as.numeric(tab$tFirst.date[tab$cp]))
  ywerte <- rep(max(datrise$hour.dec), sum(!is.na(tab$stationary)))
  xwerte <- tab$tFirst.date[!is.na(tab$stationary)]
  stationary <- tab$stationary[!is.na(tab$stationary)]
  points(xwerte,ywerte , pch=15, col=c("orange", "blue")[as.numeric(stationary)+1])
  #text(tab$tFirst.date, rep(max(datrise$hour.dec), nrow(tab))-0.05, tab$phase, cex=0.7)
```

```
  points(tab$tFirst.date, rep(max(datrise$hour.dec), nrow(tab))-0.05, pch=15, col=tab$phase, cex=0.5)
  par(new=TRUE)
  plot(datset$tFirst.date, datset$hour.dec, type="l", main=log_code, col="blue", xlim=as.numeric(range(tab$tFirst.date)), ylab=NA)
  par(new=FALSE)
  plot(tab$tFirst.date, tab$diffbeta, xlim=as.numeric(range(tab$tFirst.date)), pch=16, cex=0.7, ylab="diff slope", col=c("orange",
"blue")[tab$type])
  abline(h=0)
  abline(v=as.numeric(tab$tFirst.date[tab$cp]))
  plot(tab$tFirst.date, tab$slopelon, xlim=as.numeric(range(tab$tFirst.date)), pch=16, cex=0.7, ylab="slope", col=c("orange",
"blue")[tab$type])
  #lines(tab$tFirst.date, tab$beta.future)
  abline(v=as.numeric(tab$tFirst.date[tab$cp]))
  plot(tab$tFirst.date, tab$lon, xlim=as.numeric(range(tab$tFirst.date)), type="l", ylab="latitude (or), longitude (bl)", col="blue")
  par(new=TRUE)
  plot(tab$tFirst.date, tab$lat, xlim=as.numeric(range(tab$tFirst.date)), type="l", ylab="latitude (or), longitude (bl)", col="orange")
  dev.off()
}
write.table(dat, "R:/Auswertungen/Geolocator/BarnSwallow/data/positions2_8_w20det_cp_phasen.txt", row.names=FALSE, sep="\t")
#
#------------------------------------------------------------------------------
# 4) merge stationary periods with a lox-distance < moddist
#------------------------------------------------------------------------------
#
setwd("R:/Auswertungen/Geolocator/BarnSwallow/data/") # workstation vowa
dat <- read.table("positions2_8_w20det_cp_phasen.txt", header=TRUE, sep="\t")
dat <- dat[order(dat$logCode, dat$tFirst.date),]
dat$equinox <-(dat$dayofyear >= 245 & dat$dayofyear <= 287)| (dat$dayofyear>=58 & dat$dayofyear<= 100) # plusminus 21 days
moddist <- 200 # if two modus are closer than moddist, the two consecutive sites are merged
dat$rownumber <- 1:nrow(dat)
datw <- dat[dat$posweightdet>0 & !dat$equinox,]   # filtered dat
datpsite <- aggregate(datw$lon, list(site=datw$phase, logCode=datw$logCode), ownmode)
names(datpsite)[names(datpsite)=="x"] <- "lon"
datpsite$lat <- aggregate(datw$lat, list(site=datw$phase, logCode=datw$logCode), ownmode)$x
datpsite$n <- aggregate(datw$lat, list(site=datw$phase, logCode=datw$logCode), length)$x
datpsite$stationary <- aggregate(as.numeric(datw$stationary), list(site=datw$phase, logCode=datw$logCode), median)$x
datpsite$n_lat <- aggregate(datw$lat, list(site=datw$phase, logCode=datw$logCode), function(x) sum(!is.na(x)))$x
# merge sites
datpsite <-datpsite[datpsite$n>4,]
datpsite$site[datpsite$logCode=="1SU"]
datpsite$n[datpsite$logCode=="1SU"]
datpsite$sitemerged <- datpsite$site
datpsite$distcentr <- NA
for(ind in levels(factor(datpsite$logCode))){
  index <- datpsite$logCode==ind
  if(sum(index)<2) next
  for(i in 1:(sum(index)-1)){
    if(is.na(datpsite$stationary[index][i])|is.na(datpsite$stationary[index][i+1])) next  # unknown
    if(datpsite$stationary[index][i]<0.5|datpsite$stationary[index][i+1]<0.5) next  # migration
    if(is.na(datpsite$lat[index][i])|is.na(datpsite$lat[index][i+1])) next  # unknown
    distbetweencentroid <- distCosine(c(datpsite$lon[index][i], datpsite$lat[index][i]), c(datpsite$lon[index][i+1],
datpsite$lat[index][i+1]))/1000
    if(distbetweencentroid< moddist) datpsite$sitemerged[index][i+1] <- datpsite$sitemerged[index][i]
    if(distbetweencentroid>=moddist) datpsite$sitemerged[index][i+1] <- datpsite$sitemerged[index][i]+1
    datpsite$distcentr[index][i] <-  distbetweencentroid
    write.table(datpsite, file="datpsite_withsitemerged.txt", row.names=FALSE)    # sicherungskopie (just in case)
  }
}
# include in dat
dat$sitemerged <- datpsite$sitemerged[match(paste(dat$logCode, dat$phase), paste(datpsite$logCode, datpsite$site))]
datw$sitemerged <- datpsite$sitemerged[match(paste(datw$logCode, datw$phase), paste(datpsite$logCode, datpsite$site))]

# fill the movement periods between two equal stationary sites with this site
dat$sitemerged_filled <- dat$sitemerged
for(i in levels(dat$logCode)){
  for(j in unique(dat$sitemerged[dat$logCode==i])){
    if(is.na(j)) next
    erstezeile <- min(dat$rownumber[dat$logCode==i & dat$sitemerged == j], na.rm=TRUE)
    letztezeile <- max(dat$rownumber[dat$logCode==i & dat$sitemerged == j], na.rm=TRUE)
    dat$sitemerged_filled[dat$rownumber>=erstezeile & dat$rownumber<=letztezeile] <- j
  }
}
write.table(dat, file="R:/Auswertungen/Geolocator/BarnSwallow/data/positions2_8_w20det_cp_phasen_sitesmerged1.txt",
row.names=FALSE, sep=";")
#
# end --------------------------------------------------------------------------------------------------------------------------------------
```

Figure S1: Example of a light curve recorded by the geolocator (SOI GDL2.11). The blue lines represent the light intensity recorded. Day- and nighttime can be clearly recognized on the right side of the graph. We assumed that the abrupt drop in light intensity on the 21.4.2011 marks the first visit to the nest site. The next to 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.



M2: Sex differences in the effects of the position of the sub-Saharan residence area 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, $F_{1,55} = 0.05$, $p = 0.82$).

M3: Comparison of sex-specific variances between the phenological events during the non-breeding period

Results (and R-code) of ANOVA for departure and arrival events including all possible individuals (cf. Tab.1)

Comparing the four events:

```
> leveneTest(c(resBdepmales, resNBarrmales, resNBdepmales, resBarrmales),
+          group=factor(rep(c("Bdep", "NBarr", "NBdep", "Barr"), times=c(n1males,n2males, n3males,
n4males))))
Levene's Test for Homogeneity of Variance (center = median)
       Df F value    Pr(>F)
group   3  12.736 1.048e-07 ***
      220
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
>
> leveneTest(c(resBdepfemales, resNBarrfemales, resNBdepfemales, resBarrfemales),
+          group=factor(rep(c("Bdep", "NBarr", "NBdep", "Barr"), times=c(n1females,n2females, n3females,
n4females))))
Levene's Test for Homogeneity of Variance (center = median)
       Df F value  Pr(>F)
group   3   3.901 0.01103 *
      102
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

⇨ at least one significant differences between the four events

Comparing males and females pairwise for each event:

```
> leveneTest(c(resBdepmales, resBdepfemales), group=factor(rep(c("male","female"), times=c(n1males,
n1females))))
Levene's Test for Homogeneity of Variance (center = median)
      Df F value  Pr(>F)
group  1  6.1125 0.01513 *
      99
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
> leveneTest(c(resNBarrmales, resNBarrfemales), group=factor(rep(c("male","female"), times=c(n2males,
n2females))))
Levene's Test for Homogeneity of Variance (center = median)
      Df F value Pr(>F)
group  1  0.0269   0.87
      90
> leveneTest(c(resNBdepmales, resNBdepfemales), group=factor(rep(c("male","female"), times=c(n3males,
n3females))))
Levene's Test for Homogeneity of Variance (center = median)
      Df F value Pr(>F)
group  1  0.7162 0.4003
      69
> leveneTest(c(resBarrmales, resBarrfemales), group=factor(rep(c("male","female"), times=c(n4males,
n4females))))
Levene's Test for Homogeneity of Variance (center = median)
      Df F value Pr(>F)
group  1  0.0179 0.8941
      64
```

⇨ significant difference only for the first event.

Table S1: Sex specific variances for the departure times from and the arrival times at the breeding grounds and sub-Saharan residence areas.The table shows the variance and standard deviations of the residuals from ANOVAs fitted to sex-specific data using year, population and their interaction as explanatory variables

event	*males means*	*females means*	*males s.d.*	*females s.d.*
departure breeding	19.8	58.6	4.5	7.7
arrival non-breeding	73.5	61.7	8.6	7.9
departure non-breeding	132.4	198.3	11.5	14.1
arrival breeding	128.7	123.7	11.3	11.1

M4: Comparison of the positions of the sub-Saharan residence areas between years, sex and populations using a randomiation test

Median location of the 59 individuals in 2011 was (lat. 7.0°, lon. 12.8°,) and of the 33 individuals in 2012 it was (3.2°, 15.3°). The median in 2012 was 506 km further to the SE than in 2011.

When assigning the year randomly to the individuals repeatedly (R = 4999 times), the median distance in the location was 139 km. The observed distance of the median position between to years (506km) was significantly higher than expected by chance (p=0.002).

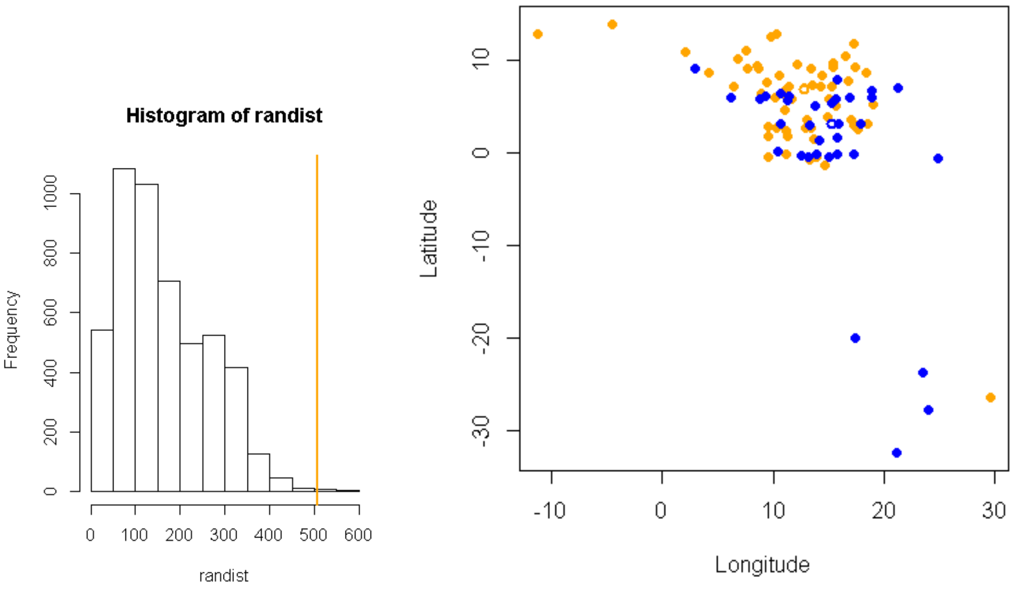


Fig: a) random distances, observed=orange, b) location of the individuals in 2011 (orange) and 2012 (blue), open circles = median location.

For comparing the sub-Saharan residence areas between the sexes and the populations, we corrected for the year-difference by shifting the locations of 2011 by 506 km to the SE, so that the median locations of the two years coincided. In the figure, we still see a year-effect. Unfortunately, comparison within a year is based on very low sample sizes.

Table S2: Comparison of the positions (latitude and longitude) of sub-Saharan residence areas between sexes and populations using a randomisation test (4999 iterations). For the six groups (3x2) differences between the median positions (km) and p-values for differences are given (M=males, F = females).

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
SE-pop M									215	0.700

There is no significant difference in the median position between any group:

Figure S1: Distribution of stationary sites south of the Sahara (<23.5° N) of individuals with more than one non-breeding range. For each individual (n=22) the position of the mode of the kernel densities (see Methods) (point) 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. The four graphs are grouped according to year (above-below) and sex (left – right). Colours represent populations (see legend).

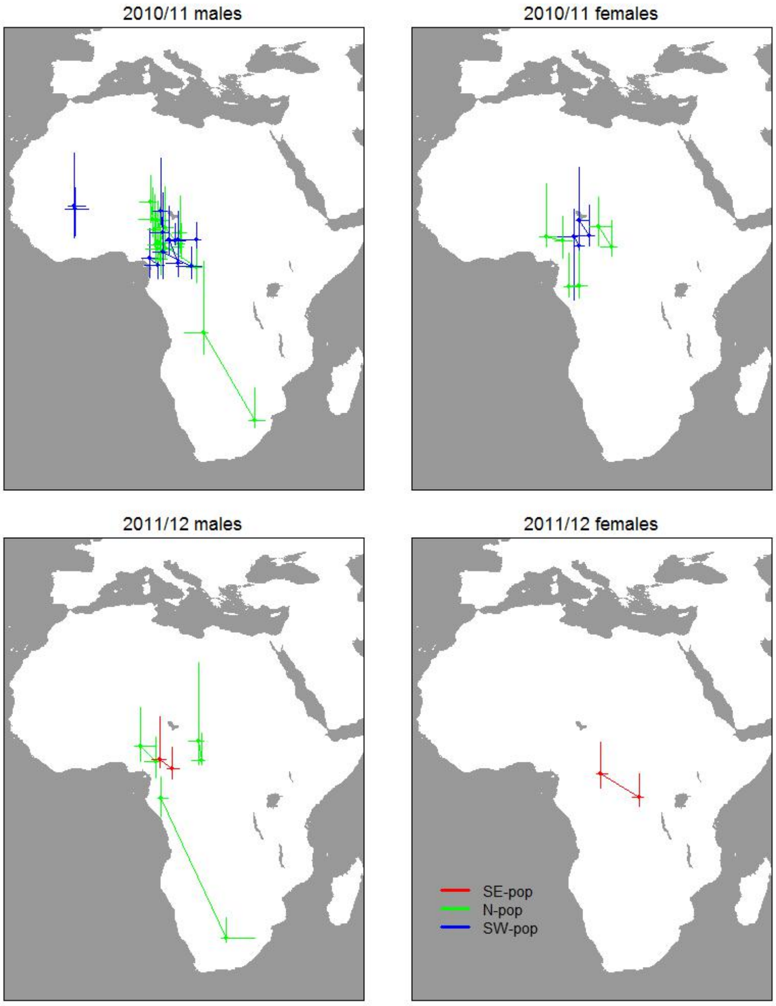
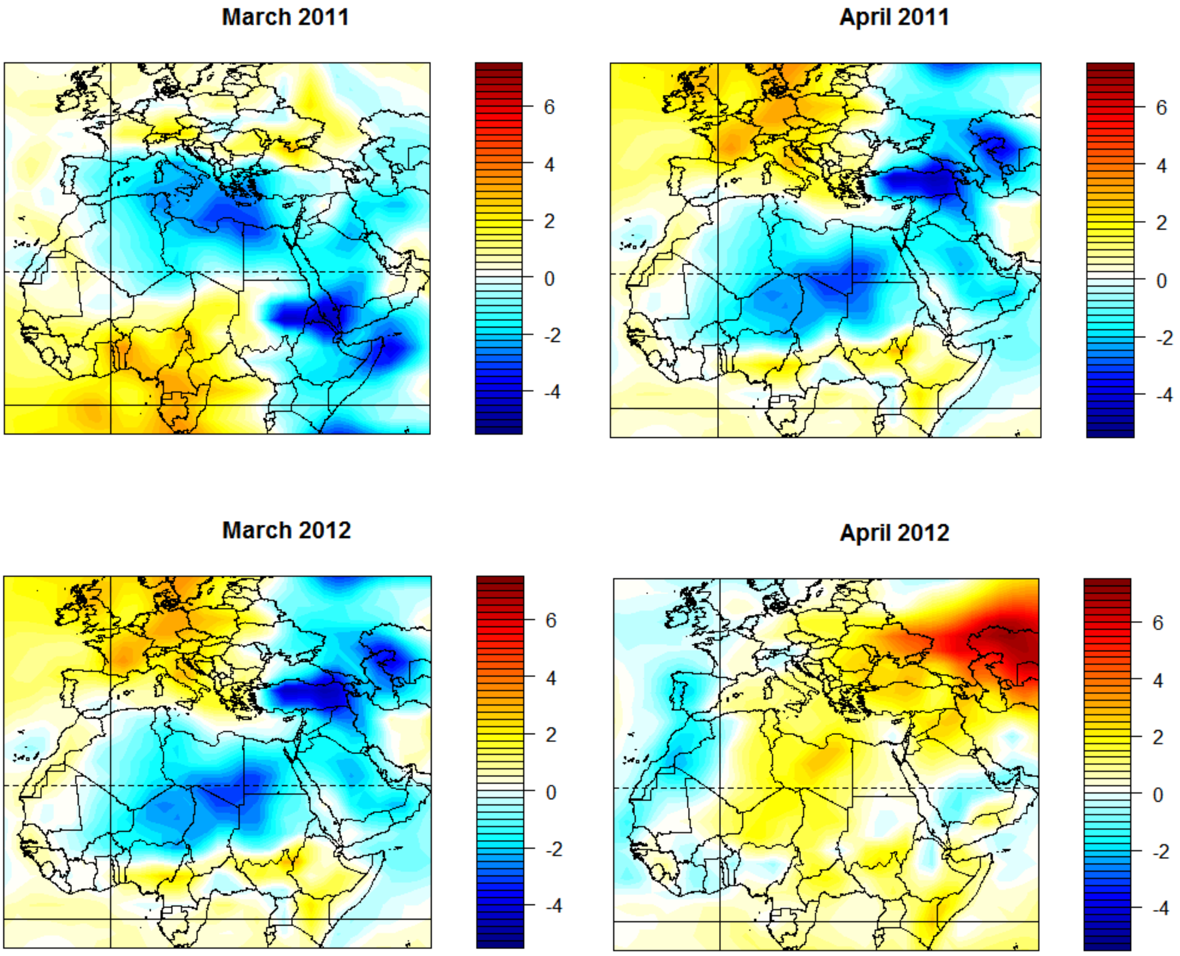


Figure S2. March-April temperature anomalies across the barn swallow wintering and migration range in the two years of study. Anomalies are expressed as the deviation (in °C) from the long-term (1960-2013) monthly mean values. Original data were gridded on a 5x5° grid and were downloaded from the NOAA-NCDC-GHCN website (iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/.GHCN/.v2).



Chapter 2

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

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ABSTRACT

Miniaturized light-level geolocators may revolutionise the study of avian migration. However, there are increasing concerns that they might negatively affect fitness. We investigate 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 with 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 days) 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.

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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, Gomez et al. 2013).

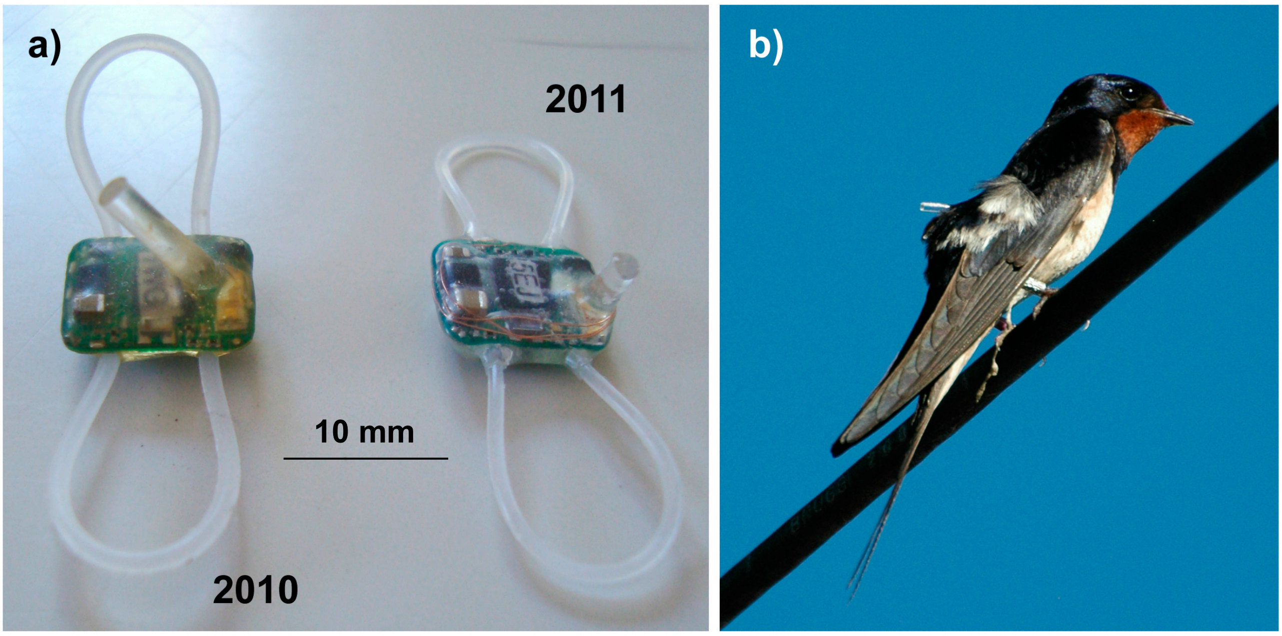

Figure 1. Picture of a) geolocator models deployed in 2010 (SOI-GDL2.10) and 2011 (SOI-GDL2.11); the difference in light stalk length and bending can be easily appreciated (see also Appendix 1); and b) a male barn swallow equipped with geolocator model SOI-GDL2.10.

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*, one of the smallest species to which geolocators have been applied to date (see Bridge et al. 2013). Barn swallows were fitted with two different geolocator models, which differed in their external size and shape and were deployed using leg-loop harnesses (Fig. 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 days) 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 Institute) 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 (see 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). In the year of geolocator deployment, geolocator and control subjects did not differ in laying date, clutch size, or age (see 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. in prep.). Preliminary inspections of African wintering sites indicated a broad overlap with the known wintering range of the study population derived from ring recoveries (see 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 days 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 (see 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.

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 (see 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 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, were 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 (d.f.) 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 days, mean age = 10.5 (2.0 s.d.) 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 days before nestling measurement and when nestlings were a maximum of 4 days 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 (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 geolocator 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* (see Appendix 5).

On the whole, there was no conclusive evidence that different harness configurations affected survival independently of geolocator

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)	-

loss, and there was no effect of geolocator weight (either absolute or relative, expressed as % body mass) on survival (see 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 3). 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 Fig. 1) did not markedly reduce the negative effects of geolocator deployment on survival, as confirmed by models including

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) F: 5.11 (2.77-9.42)	0.30 (0.49)	M: 1.85 (1.07-3.19) 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

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 the 2010 ones (Table 2). Wing length or age did not differentially affect survival of geolocator and control subjects (see Appendix 5).

Finally, geolocator weight (either absolute or relative) did not significantly affect survival of geolocator subjects of either sex (Appendix 6).

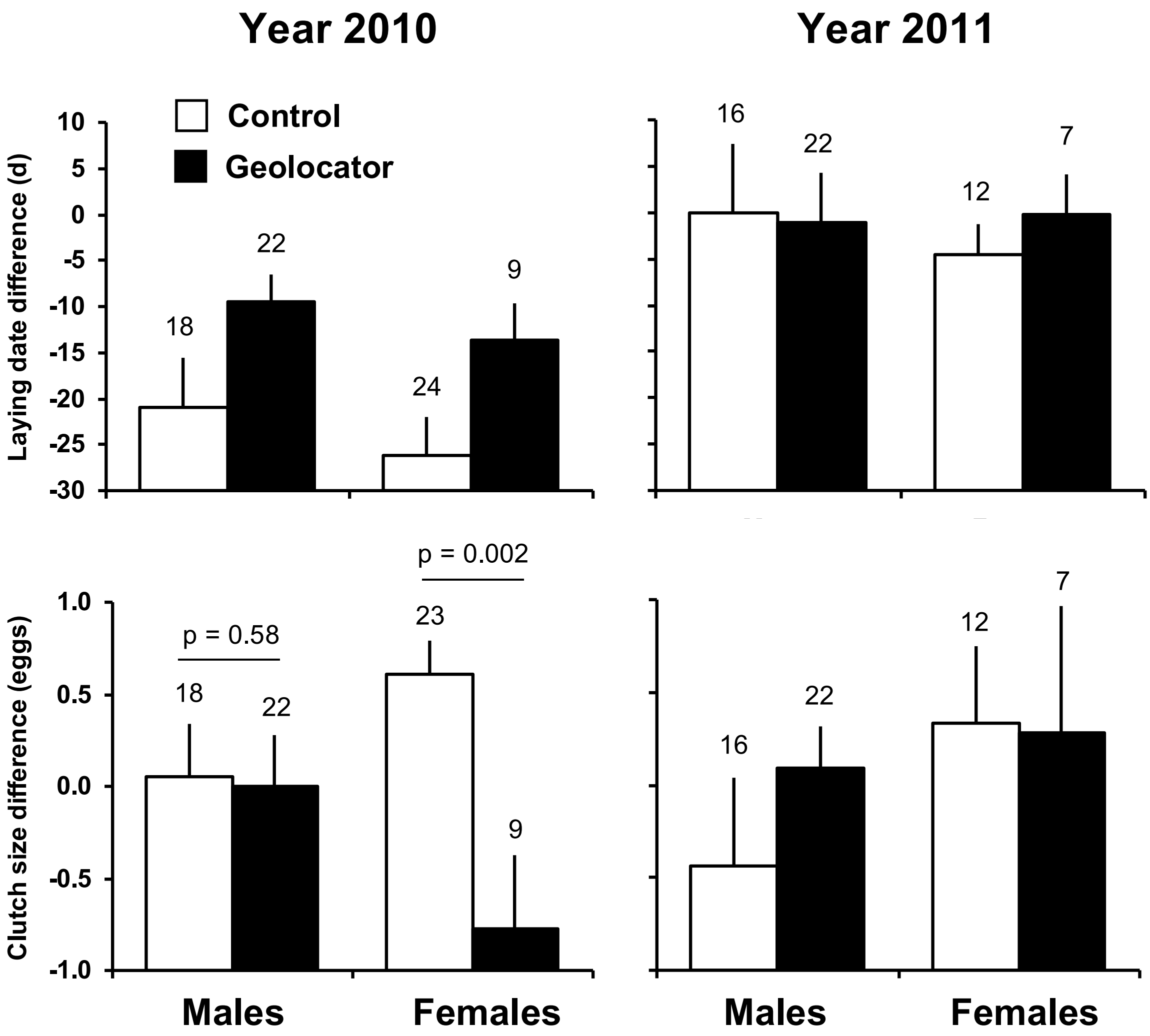

Figure 2. Within-subject differences (value in year *i* + 1 minus value in year *i*) of laying date and clutch size in relation to geolocator deployment and sex (mean + s.e.) in the two study years (year *i*) (see Table A2 for details of statistics). Numbers above bars indicate samples sizes, and may 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.

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 (Fig. 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 (Fig. 2, Table A2). However, deployment of geolocators on males did not significantly affect the clutch size laid by their partner (Fig. 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 (Fig.

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).

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, Fig. A1), nor fledging success (brood size at fledging) (Table A3, Fig. A1). Therefore, geolocators did not negatively affect reproduction in the short-term.

DISCUSSION

Our analyses indicate that geolocator deployment 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 in either sex. Lower annual survival of controls in the second compared to the first (Table 1), reflecting poor ecological conditions during migration and/or wintering, may have partly obscured any reduction of the impact of the streamlined geolocator 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, pers. obs.; see also Fig. 1), and impaired escape performance, especially of females, leading to higher predation and decreased annual survival. A final possibility, that geolocator birds have lower breeding site fidelity than controls, can be dismissed because of the strong breeding philopatry of the barn swallow (see 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.

Bird 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 fedging success (see also Gomez et al. 2013). This latter finding was obtained when parents were equipped with the heavier and less aerodynamic 2010 model, so that we can 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, suggest 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. We suggest that studies aiming at deploying geolocators or other year-round tagging devices (e.g. GPS or satellite transmitters) should be preceded by pilot experiments involving treated and control subjects. Clearly, the design of year-round tagging devices should be improved to further minimize negative impacts, as even minor differences in weight and drag can make the difference.

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SUPPLEMENTARY ONLINE MATERIAL

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. Sampe 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 withouth 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 differentialy 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, $z = 0.42$, $p = 0.67$).

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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.

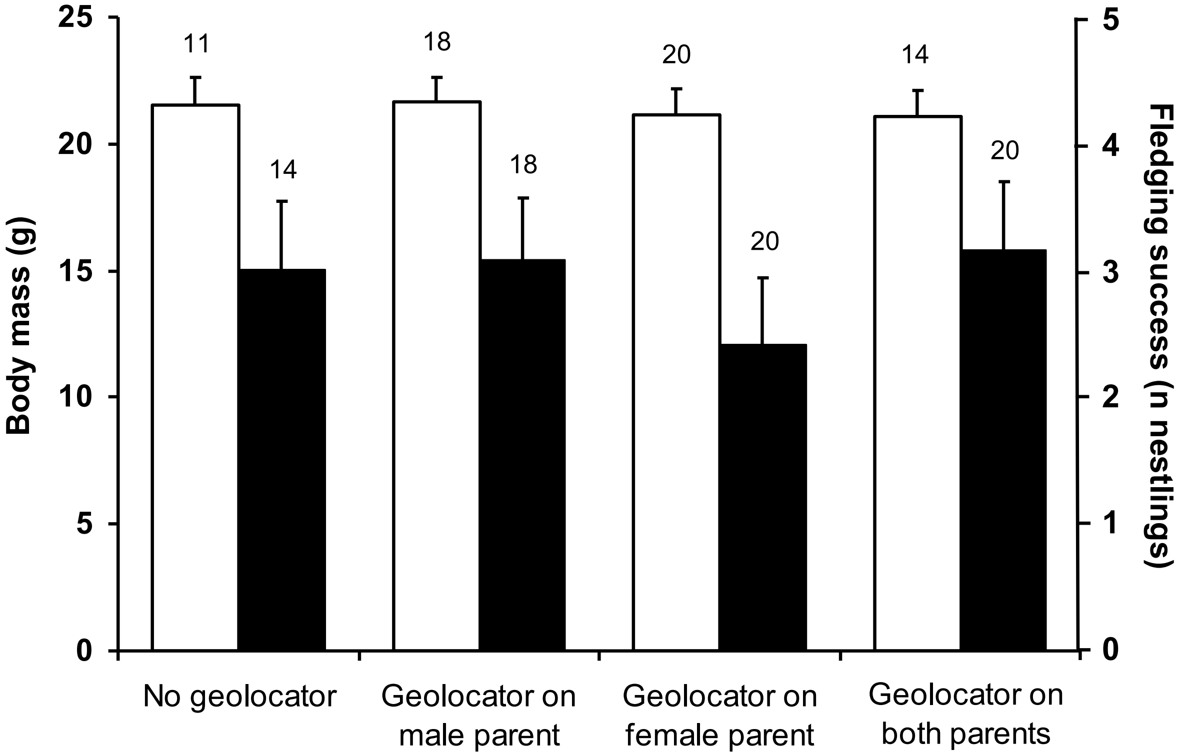
	Year 2010				Year 2011			
	Estimate (s.e.)	F	d.f.	p	Estimate (s.e.)	F	d.f.	p
Laying date (days)								
Treatment	11.93 (4.57)	6.81	1, 69	0.011	3.11 (6.89)	0.20	1, 40	0.65
Sex	4.85 (4.53)	1.14	1, 69	0.29	1.03 (6.84)	0.02	1, 52	0.88
Treatment × sex	-1.11 (9.29)	0.01	1, 69	0.91	-6.45 (13.37)	0.23	1, 49	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)
geolocaotor 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.



PART 2

NATAL DISPERSAL

Chapter 3

Context-, phenotype-, and kin-dependent natal dispersal of barn swallows (*Hirundo rustica*)

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Original Article

Context-, phenotype-, and kin-dependent natal dispersal of barn swallows (*Hirundo rustica*)

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Natal dispersal is a major life-history trait, with important consequences for population dynamics and genetic structure. Successful dispersal depends on a complex blend of decisions at all main stages of the dispersal process: emigration, prospection for a site, and settling. Costs and benefits of such decisions are expected to depend on sex and on the ecological context, on individual physiological state, and on concomitant decisions by relatives, which affect competition with kin and inbreeding. We analyzed natal dispersal propensity (i.e., dispersing or not) and dispersal distance in the semicolonial barn swallow (*Hirundo rustica*) in relation to context-, phenotype-, and kin-dependent factors. Females had larger dispersal propensity and distance than males. Dispersal propensity of both sexes was negatively density dependent and was less likely from colonies (farms) with large number of livestock, which is important to barn swallow distribution. Dispersal propensity was larger among males ranking high in the body mass brood hierarchy and smaller among late-hatched females. Dispersal distance was larger for late-hatched males and for females that ranked high in the body mass brood hierarchy. Finally, both dispersal propensity and distance of males increased with the number of male siblings. We, thus, identified several context-, phenotype-, and kin-dependent components of dispersal decisions. Phenotype-dependent effects suggest that decisions of whether to disperse and of dispersal distance are different processes under control of sex-specific traits. Finally, male dispersal behavior suggests that kin selection favors males that reduce the risk of sib–sib mating competition, in a population with male-biased tertiary sex ratio.

Key words: **body mass, dispersal, habitat quality, hatching date, sex.**

INTRODUCTION

Natal dispersal is a major life-history trait and has pervasive consequences for the dynamics and the genetic structure of populations, as well as for species distribution and thus community composition (Greenwood 1980; Johnson and Gaines 1990; Clobert et al. 2001; Hanski and Gaggiotti 2004; Bowler and Benton 2005). Natal dispersal is essentially a 3-step process, which involves emigrating (or not) from the natal place, moving through an unknown region, and settling to breed (Hanski and Gilpin 1997; Bowler and Benton 2005). Decisions at each of these steps can entail both costs and benefits (Massot and Clobert 2000; Clobert et al. 2001; Ims and Hjermann 2001; Bonte et al. 2012) and can have dramatic consequences for an individual's fitness both directly and via the effects on kin, in terms of competition or inbreeding. Dispersal decisions, thus, typically depend on several factors acting at different scales and stages of the decision and also in a sex-dependent way (Clobert et al. 2001).

Habitat quality, also including fragment size and isolation, and density-dependent competition for limiting resources and mates are tightly linked factors that have been traditionally identified as fundamental "context-dependent" (or "condition-dependent" according to Clobert et al. 2009 terminology) determinants of dispersal decisions (Hanski and Gilpin 1997; Paradis et al. 1998; Matthysen et al. 2001; Massot et al. 2002; Kennedy and Ward 2003; Doligez et al. 2008; Balbontín et al. 2009; Clobert et al. 2009; Gerrard et al. 2012). The paradigm of habitat choice theory is negative density dependence in settling decisions mediated by competition (Fretwell and Lucas 1970; Rosenzweig 1981; Greenwood and Harvey 1982; Martin and Martin 2001; Bowler and Benton 2005; see Clobert et al. 2001). However, in several situations positive, rather than negative, density dependence may occur. Such conspecific (or heterospecific) "attraction" may result from presence of other individuals revealing a high-quality habitat and from social effects, making risk of predation or parasitism smaller (Serrano et al. 2003;

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Danchin et al. 2004; Doligez et al. 2004; Donahue 2006; Fletcher 2007; Parejo et al. 2008). Thus, occurrence of positive or negative density-dependent dispersal may considerably vary among species/populations (Matthysen 2005; see Mönkkönen et al. 1999 for nonlinear density dependence).

Dispersing individuals are expected to take the "personal" information that they can acquire about ecological and demographic conditions at potential settling sites and the concomitant decisions by other individuals of the same cohort (Nicolaus et al. 2012) into account. A major role in adaptive dispersal decisions has been invoked for "social" information that can be extracted from individuals of the same or other species (Danchin et al. 2001, 2004; Valone and Templeton 2002; Doligez et al. 2003; Dall et al. 2005; Seppanen et al. 2007). Special attention may also have to be paid to dispersal decisions by related individuals. In fact, risk of inbreeding is an evolutionary driver of sex-biased dispersal (Greenwood 1980; Léna et al. 1998; Perrin and Mazalov 1999). In addition, dispersal can affect competition among kin for limiting resources and mates, also depending on tertiary sex ratio (Hamilton and May 1977; Saino et al. 2013). Risk of inbreeding and competition with kin should result in larger natal dispersal. Yet, kin selection may reduce dispersal if relatives provide favorable social conditions or when offspring increase their inclusive fitness by participating in cooperative breeding systems with kin (Brown 1987; Cockburn 1996).

In turn, phenotype-dependent dispersal (see Clobert et al. 2009) may arise from variation in physiological state or morphology, which can affect the costs-to-benefits balance of dispersal (Nunes and Holekamp 1996; Belthoff and Dufty 1998; Barbraud et al. 2003; see also Balbontín et al. 2009), or in explorative and social behavior (Clobert et al. 2009). A seldom considered source of variation in phenotype-dependent dispersal is maternal effects via egg quality (Mousseau and Fox 1998). Mothers may epigenetically prime behavioral or other traits relevant to dispersal, such as exploratory behavior, by modulating egg composition in terms of hormones with developmentally entrenched effects (Tschirren et al. 2007; Badyaev 2008; see also Dingemanse et al. 2003). In addition, parental decisions over the site and time of breeding may generate variation in traits that can influence dispersal ability/propensity (Nilsson 1989; Altwegg et al. 2000).

Individual dispersal decisions should, thus, depend on the expected fitness reward of any dispersal strategy as influenced by the independent and combined effects of context-, habitat-, and kin-dependent factors (Clobert et al. 2009; Bonte et al. 2012). Yet, few studies have attempted a comprehensive analysis of the effects of such diverse factors on dispersal.

In the present study, we focus on dispersal propensity and dispersal distance in relation to context- (colony size and habitat quality), phenotype- (body mass relative to siblings), and kin-dependent (sibling sex) effects and to maternal effects (hatching date) of young of a semicolonial, socially monogamous passerine bird, the barn swallow (*Hirundo rustica*). Barn swallows breed most often in farms with livestock (Møller 1994; Ambrosini et al. 2002; Turner 2006). Because suitable nesting sites are clustered in farms scattered within a farmland matrix, which is unsuitable for nesting, the barn swallow is an excellent model to investigate dispersal among habitat patches. In most barn swallow populations (including the present one), *breeding* dispersal distance is very small (Møller 1994; our unpublished data; see Schaub and von Hirschheydt 2009), whereas natal dispersal is the rule (Møller 1994; Turner 2006), although considerable variation in dispersal propensity exists among geographical populations (Balbontín et al. 2009).

As context-dependent predictors of dispersal, we considered colony size and number of livestock at the natal site (recorded in the year of both birth and recruitment), and mean breeding success at the natal colony in the year of birth. The large majority of barn swallows breed in colonies of 2 to tens of pairs (Møller 1994; Cramp 1998). Population size has sharply declined in southern Europe (Burfield and Van Bommel 2004; Maumary et al. 2007; Ambrosini et al. 2012) due to changes in farming practices (Sicurella et al. 2013) and due to deterioration of ecological conditions during migration or wintering in Africa (Robinson et al. 2008). If population size is controlled by factors that act during the nonbreeding period, local competition at breeding colonies may be relatively mild. We, therefore, expected dispersal propensity to negatively covary with original colony size because colony size may be positively correlated with habitat quality but only weakly correlated with intensity of competition. Similarly, because barn swallows prefer farms housing livestock (Møller 2001; Grüebler et al. 2010; Ambrosini et al. 2012), we predicted dispersal to be less likely from farms with larger numbers of livestock. Because breeding success may provide social information on habitat quality (Danchin et al. 2001; Ward 2005), we also expected dispersal to be less likely from colonies with high breeding success.

As for most birds, female barn swallows have larger dispersal propensity than males (Greenwood and Harvey 1982; Møller 1994; Balbontín et al. 2009), suggesting that the payoff of dispersing is larger for females. Body condition and viability of barn swallow offspring decline with hatching date (Møller 1994; Saino, Romano, Ambrosini, et al. 2012). Any physiological cost of dispersal may, therefore, be exacerbated by late hatching, leading to predict shorter dispersal among late-hatched females. Moreover, if late hatching predicts late arrival from spring migration because of tight annual routines or poor migration performance, fewer opportunities to prospect alternative colonies by late-hatched/late-arriving females can increase natal philopatry. The same arguments apply to males, though their larger natal philopatry suggests smaller selective advantage from dispersing and may produce a different pattern of covariation of dispersal with hatching date. In a nearby barn swallow population, nestling body mass relative to nest mates, rather than body mass per se, has been found to positively predict life expectancy after sexual maturity (Saino, Romano, Ambrosini, et al. 2012). Within-brood body mass rank is consistent during the nestling period and reflects laying order (Saino et al. 2001; Ferrari et al. 2006; our personal observation). We, thus, used relative body mass as a proxy for position in the size/laying-order brood hierarchy. Along the same lines of reasoning as for hatching date, we expected dispersal to positively covary with relative body mass, particularly among females.

We also addressed the question of whether brood sex composition affects dispersal. Tertiary sex ratio in the barn swallow (as in most birds) is male biased (Donald 2007; Saino et al. 2013). Individual philopatric males may, thus, have to compete with siblings for limiting mating opportunities (see also Balbontín et al. 2009). Thus, we expected a positive covariation between male dispersal propensity or distance and the absolute number of male siblings (see Pasinelli and Walters 2002). Conversely, we expected the association between dispersal and the number of female siblings to be weak because the chances of 2 opposite-sex siblings meeting at their natal colony are small, owing to large female dispersal. Finally, we tested whether dispersal distance of individuals that did disperse was predicted by phenotype-dependent variables and brood sex composition (both sexes). The relationships that we expected in these analyses were of the same sign as for the analyses of dispersal propensity per se.

METHODS

Study organism

The barn swallow is a small (ca. 20 g), aerially insectivorous, long-distance migratory passerine (Møller 1994; Cramp 1998; Turner 2006). Adults arrive to their European breeding quarters in February/May. Breeding occurs semicolonially, mostly inside rural buildings (e.g., cowsheds, garages). Socially monogamous pairs have 1–3 clutches of 2–7 eggs per breeding season. Hatching asynchrony is small, though nonnegligible. Altricial nestlings fledge when approximately 18–20 days old and are attended by parents for some days after fledging, but may stay few weeks at their original colony before undergoing premigratory dispersal. In southern Europe, breeding covers up to 5 months (April–August). Autumn migration (August–October) leads swallows to their wintering range in sub-Saharan Africa. Currently available estimates of natal dispersal distance are in the order of 5 km for males and 10 km for females (Turner 2006), but natal dispersal probably varies among geographical regions according to orography and distribution of suitable breeding sites, and estimates also depend on sampling design (see Balbontín et al. 2009).

Field methods

We studied barn swallows in 2009–2012 at a total of 38 colonies (= farms) located in the Magadino Plain (southern Switzerland, barycenter of the study farms: 46°9′54″N, 8°55′47″E). The study area is approximately rectangular (10 × 4 km) and mainly consists of farmland (Figure 1). The study area occupies the bottom of the large Alpine valley of the Ticino river. Dispersal outside the study area can occur northeast, along the Ticino valley itself, and west and southwest along the banks of Lake Maggiore where breeding barn swallows are common, but also north and south, on the slopes of the surrounding mountains and lateral valleys, where barn swallow colonies also occur (personal observation). The landscape in the study area is dominated by maize and hay fields. In all years, we intensively ringed the nestlings (*n* = 579, 1248, and 1353 in 2009, 2010, and 2011, respectively). All the nests in each farm were inspected every 10–12 days to record breeding events and measure nestling body mass (nearest 0.1 g; expressed in g × 10). Hatching date could be either directly identified on nest inspection or estimated by means of several cues (see Ambrosini and Saino 2010). Any inaccuracy in age estimates would be of ±1 days in the large majority of the cases (see Ambrosini and Saino 2010) and thus negligible, given that estimated hatching dates in present sample of broods spread over 108 days (standard deviation [SD] = 23.1 days, *n* = 279).

To identify local recruits, in 2010–2012, we intensively captured the adults by placing mist-nests before dawn at the exits of the rural buildings where barn swallows usually spend the night during the breeding season. Because this method is highly effective, we are confident that we missed catching extremely few adults, if any, in every year (see e.g., Saino, Romano, Ambrosini, et al. 2012; Saino et al. 2013).

We recorded GPS position of the center of each colony and thus distance (approximation of 50 m) between each pair of colonies, colony size (number of breeding pairs), number of livestock (cows or horses) at the farm, and breeding success (brood size at last visit to the nest; 2010 and 2011 only) in each nest. In a subsample of broods, we also identified the sex of individual nestlings by means of molecular techniques using DNA extracted from small blood samples (Saino et al. 1999, 2008). Molecular sexing could not be successfully performed for 4 out of 390 nestlings that fledged from this subsample of broods.

We will refer to the individuals that were ringed as nestlings and were recruited as breeding adults in their colony of origin as to "philopatric individuals" and to individuals that were recruited in a colony different from that of origin as to "dispersing individuals." In the analyses, "dispersal propensity" (dispersing or not dispersing from the natal colony) was coded as 0 for philopatric

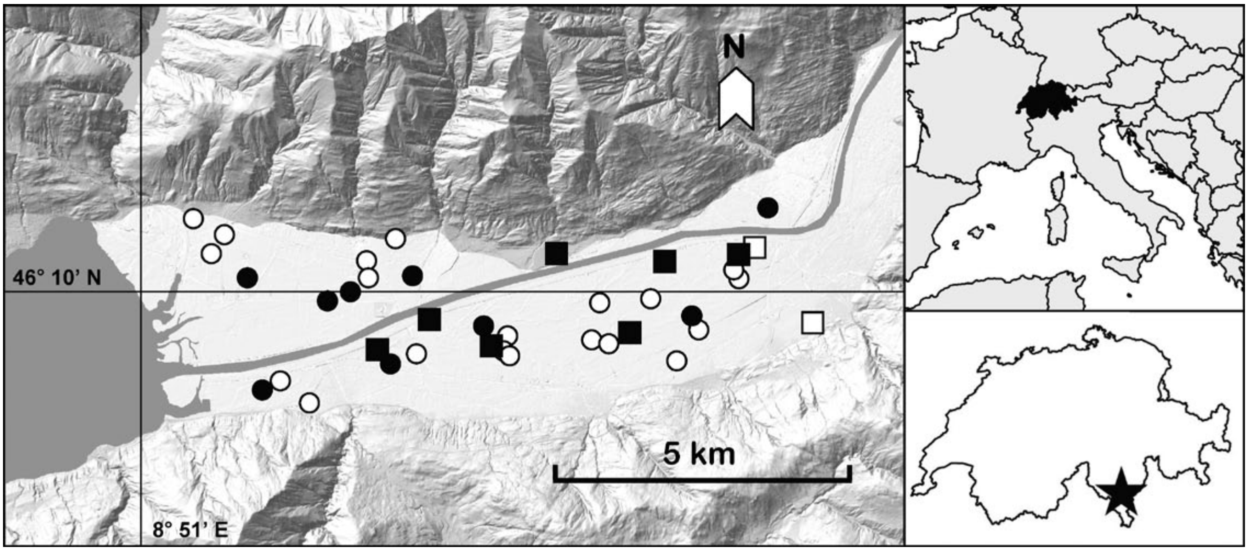

Figure 1

Map of the study area in southern Switzerland (Magadino Plain) showing the position of the study farms. The maps on the right show the position of Switzerland within Europe (upper panel) and the position of the study area within Switzerland (black star, lower panel). Symbols reflect colony size (breeding pairs; mean 2010–2012): white circles: 1–5 breeding pairs; black circles: 6–10; white squares: 11–15; black squares: >15.

individuals or 1 for dispersing individuals. Dispersal distance (in m) is the distance between the colony of origin and the colony of recruitment.

Statistical analyses

We analyzed dispersal in relation to sex (factor), hatching date, body mass relative to the brood mean, colony size, number of livestock, and mean breeding success at the colony site (covariates) by simple or multiple binomial linear mixed models where colony of origin and year of recruitment were always included as random effects. Colony size and number of livestock ($\log_{10}(x + 1)$ transformed to reduce leverage by extreme livestock number data) were computed both for the year of birth and for the year of recruitment, but the data for either year were included in separate analyses because of collinearity. Dispersal distance was analyzed in generalized linear mixed models (GLMM) assuming a geometric distribution (Buechner 1987; assuming an exponential distribution led to virtually identical results). In all models, we also controlled for overdispersion. Because nestling ringing effort and distribution varied among years and farms, throughout the text, we refrain from making inferences on the statistical effects of random factors, which were thus considered as "nuisance variables" that account for dependency of observations from the same year or farm. Inclusion of a random factor "sibship" was impractical due to the small number of cases in which 2 recruits originated from the same brood (see Results). However, the effect of rearing environment was partly accounted for by that of the colony of origin.

In the analyses, relative body mass of any individual recruit when nestling was expressed as the ratio (×100) between its body mass and mean brood body mass. We did not use absolute body mass because we were mainly interested in the effect of the position of individual offspring in the age/size brood hierarchy (Saino, Romano, Ambrosini, et al. 2012) and, importantly, age at body mass measurement could not be standardized because of time and logistic constraints. However, we are confident that relative body mass at measurement reflected the rank of individual nestlings in the age/size brood hierarchy because relative body mass is consistent during the nestling period (Ferrari et al. 2006).

Because of the small number of philopatric females in an otherwise large sample of recruits, we could not test the differential effects of predictors of dispersal propensity in multiple GLMM with interaction effects between sex and the other predictor variables. We, thus, relied on tests of the interaction with sex for each predictor in a separate model for each predictor. Conversely, the tests on dispersal distances could be done by including all the predictors and their interaction with sex in the same model, thanks to the large number of dispersing individuals of both sexes.

All the variables that were simultaneously entered in the multiple GLMM were scrutinized for collinearity, which never appeared to be an issue as correlation coefficients were always <0.60.

Because of the relatively small number of cases of local recruitment of siblings, and the fact that these cases were scattered among several different farms of origin and of recruitment, no analysis of dispersal behavior of siblings was attempted here. In addition, because several colonies in the study area were not accessible and we therefore have no information on availability and quality of suitable breeding sites within dispersal range from each study colony, we do not investigate the effect of habitat quality at the colonies where dispersing individuals were recruited. All the analyses were run using SAS 9.2.

RESULTS

The 280 (157 males, 123 females) individuals included in the sample originated from 32 colonies (mean, SD, range of the number of recruits per colony: 8.75, 9.21, 1–34) and were recruited as breeders in 36 colonies (7.78, 9.06, 1–32). The number of recruits per year was 71 in 2010, 90 in 2011, and 119 in 2012. The proportion of ringed nestlings that were eventually recruited was 0.12, 0.07, and 0.09 in 2010, 2011, and 2012, respectively. The frequency (%) of nests of origin that generated 1, 2, and 3 recruits was 85.4, 12.1, and 2.5, respectively.

Sex difference in dispersal propensity and distance

Males were less likely to disperse than females (GLMM; fixed effect of sex: $F_{1,245} = 15.69$, $P < 0.001$; see Statistical analyses) (Figure 2). In fact, 38 out of 157 (24.2%) males but only 9 out of 123 (7.3%) females were philopatric. Dispersal distance was significantly larger for females than for males (GLMM: effect of sex: $F_{1,197} = 37.88$, $P < 0.001$; males 1.83 (0.13) km, $n = 119$; females: 3.30 (0.24) km, $n = 114$; one individual with dispersal distance of 15.5 km that was located, thanks to information by a farmer, was excluded from all analyses of dispersal distance) (Figure 2).

Predictors of dispersal propensity

Single-effect GLMM disclosed partly different patterns of variation in dispersal of either sex in relation to phenotype-dependent or context-dependent variables recorded at the colony of origin in the year of recruitment. Males were more likely to disperse when they ranked high in the body mass brood hierarchy, whereas dispersal was less likely among females that hatched late (Table 1; Figure 3). Moreover, dispersal was less likely to occur among both males and females from a large colony located in a farm with large number of livestock (Table 1; Figure 3). Breeding success (data for 2010 and 2011 only) did not predict dispersal of both sexes (Table 1).

Multiple GLMM on either sex separately confirmed the significant effects of relative body mass and of colony size on dispersal propensity of males and the significant effect of colony size on dispersal propensity of females, whereas the effect of hatching date on dispersal of females was marginally nonsignificant (Table 1). The model presented in Table 1 for males does not include breeding success because data were available only for 2 of the 3 study years (see above). However, inclusion of this variable confirmed the significant effects of relative body mass and colony size, and the nonsignificant effect of breeding success (details not shown; no multiple GLMM including colony breeding success attempted for females because of small number of philopatric females).

Separate GLMM of dispersal propensity with sex and each phenotype- or context-dependent predictor entered at a time showed a significant sex by relative body mass effect ($F_{1,240} = 5.01$, $P = 0.026$), whereas no significant interaction with sex was found for the other predictors (details not shown).

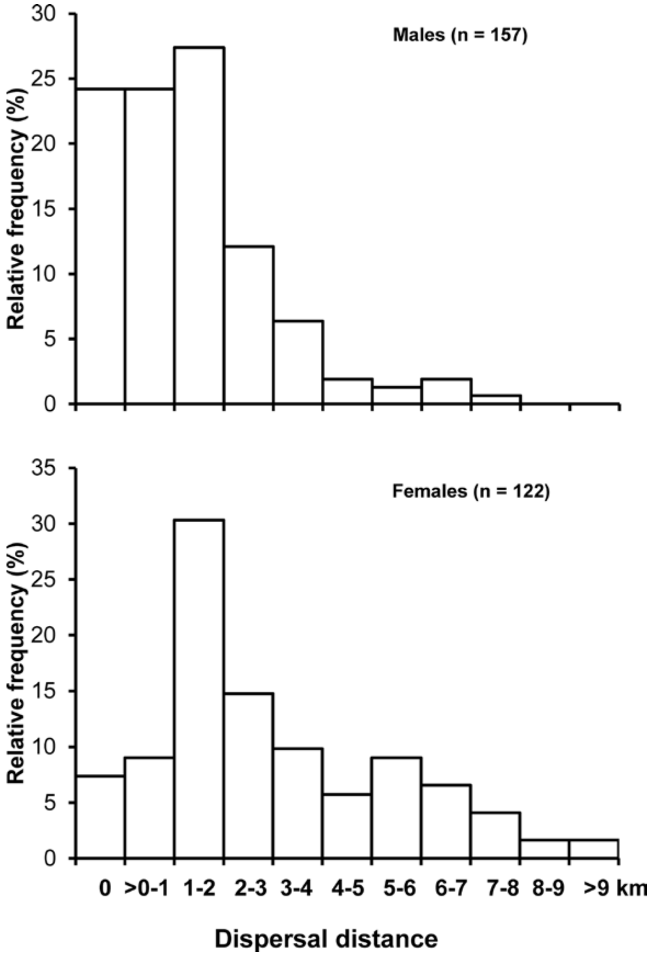

Figure 2
Frequency distribution of the dispersal distances of males and females. Class “0” indicates the relative frequency of philopatric individuals. One female with extremely large dispersal distance (15.50 km) is not represented.

We tested for any interaction between the predictors of dispersal listed in Table 1 by entering individual pairs of variables plus their interaction in separate models and found no evidence for combined effects in either of the sexes (P always >0.05; details not shown).

Simple GLMM where we included colony size and livestock farming in the year of birth rather than in the year of recruitment confirmed a significant negative effect of colony size (coefficient: −0.103 (0.036), $F_{1,92}$ = 8.15, P = 0.005) and livestock (−0.532 (0.253), $F_{1,125}$ = 4.41, P = 0.038) on dispersal propensity of males. A significant negative effect of livestock was also observed on dispersal propensity of females (−1.12 (0.55), $F_{1,93}$ = 4.12, P = 0.045), consistently with the relationships observed for the year of recruitment, whereas the effect of colony size was nonsignificantly negative (−0.16 (0.09), $F_{1,60}$ = 3.18, P = 0.079). Colony size may negatively predict dispersal because large colonies are in favorable sites (and no negative density-dependent effects occur), large aggregations of individuals are attractive, or both. In a GLMM, the proportion of philopatric recruits was significantly associated with the second-order polynomial term of colony size at recruitment (intercept = −4.782 (1.098); colony size: 0.329 (0.115), t_{29} = 2.86, P = 0.008; (colony size)^2: −0.0068 (0.0030), t_{29} = −2.27, P = 0.031). The coefficients of the fitted function imply that the proportion of philopatric individuals increased monotonically with colony size in the range of colony sizes recorded in the study, but that such increase occurred at slightly lower rate at large compared with small colony sizes (i.e., that the trend was decelerated). This finding suggests either that social attraction diminished at large colonies sizes or its effect tends to be compensated by the effect of perceived stronger competition as colony size increases.

Predictors of dispersal distance

In single-effect GLMM, males that hatched late in the season had larger dispersal distance (coefficient = 0.006 (0.003), $F_{1,88}$ = 4.22, P = 0.043; Figure 4), whereas no significant covariation of dispersal distance with relative body mass ($F_{1,87}$ = 0.02, P = 0.881) or mean breeding success at colony level (2 years only; $F_{1,70}$ = 0.30, P = 0.588) was observed. Dispersal distance of females was not predicted by hatching date ($F_{1,82}$ = 0.91, P = 0.344) or breeding success ($F_{1,40}$ = 0.93, P = 0.342), but increased with relative body mass (coefficient: 2.49 (1.00), $F_{1,82}$ = 6.18, P = 0.015).

Thanks to large number of dispersing individuals of both sexes, dispersal distance could be modeled in both sexes simultaneously. However, in the analyses of dispersal distance, the context-dependent effects at the level of original colony were not considered because we expected that these effects influenced dispersal per se (see above) but not dispersal distance. In a multiple GLMM, the 3-way interaction between sex, hatching date, and relative body mass did not predict dispersal distance ($F_{1,188}$ = 0.06, P = 0.800). A simplified model disclosed significant 2-way interactions between sex and hatching date or relative body mass (Table 2). Thus, dispersal distance increased with hatching date more among males than among females, whereas it increased with relative body mass more among females than among males.

Effect of brood sex composition on dispersal propensity and distance

We had information on sex composition of the original brood for 58 male and 36 female recruits. Fifteen (25.9%) of these 58 males but only 3 (9.1%) out of the 36 females were philopatric.

Dispersal propensity of males increased significantly with the number of male siblings, but was not influenced by the number of female siblings or by sex ratio of their siblings (Table 3; Figure 5). The effect of the number of male siblings on dispersal was significant (coefficient = 0.883 (0.428), $F_{1,42}$ = 4.25, P = 0.046) also in a model that included the effect of relative body mass. Because of small sample size, no analysis of dispersal of female offspring in relation to brood sex composition could be done.

Dispersal distance of females was not predicted by number of male or female siblings or by sex ratio of the siblings ($F_{1,33}$ < 0.63, P > 0.43 in all cases). Conversely, dispersal distance of males increased with the number of male siblings ($F_{1,56}$ = 5.31, P = 0.025, coefficient = 0.552 (0.192)) (Figure 6). An analysis of the data for both sexes showed that the effect of the number of male siblings on dispersal distance was significantly different between males and females ($F_{1,76}$ = 6.07, P = 0.016; coefficient for males: 0.442 (0.145), t_{76} = 3.05, P = 0.003, females: −0.113 (0.172), t_{76} = −0.65, P = 0.515; Figure 6). A complex model with the effects of sex, hatching date, relative body mass, and number of male siblings and all 2-way interactions confirmed the significant differential effect of number of male siblings on dispersal distance of either sex ($F_{1,69}$ = 8.12, P = 0.006) and disclosed no additional significant interaction effects.

Table 1

Single-effect and multiple binomial linear mixed models of dispersal propensity (philopatric = 0, dispersing = 1) in relation to hatching date, body mass relative to the siblings, colony size, and number of livestock (log transformed) in the year of recruitment, and mean breeding success in the colony and year of origin

	Single-effect models				Multiple models			
	Estimate (SE)	df	*F*	*P*	Estimate (SE)	df	*F*	*P*
Males								
Hatching date[a]	−0.003 (0.008)	1,125	0.14	0.707	0.002 (0.009)	1,120	0.23	0.819
Relative body mass[b]	12.54 (3.15)	1,123	15.86	<0.001	15.59 (3.55)	1,120	19.31	<0.001
Colony size[c]	−0.078 (0.034)	1,125	5.08	0.026	−0.133 (0.046)	1,120	8.19	0.004
Livestock[c]	−0.554 (0.253)	1,125	4.46	0.037	−0.430 (0.423)	1,120	1.03	0.312
Breeding success[d]	−0.012 (0.904)	1,71	0.00	0.989				
Females								
Hatching date[e]	−0.031 (0.015)	1,92	4.50	0.037	−0.027 (0.014)	1,88	3.62	0.060
Relative body mass[e]	1.332 (4.607)	1,92	0.08	0.773	2.407 (4.625)	1,88	0.27	0.604
Colony size[f]	−0.155 (0.046)	1,93	11.63	0.001	−0.136 (0.057)	1,88	5.69	0.019
Livestock[f]	−1.161 (0.562)	1,93	4.27	0.042	−0.393 (0.616)	1,88	0.41	0.524
Breeding success[g]	−1.085 (1.806)	1,62	0.36	0.550				

Farm of origin and year of recruitment were included in all models as random effects. In the "single-effect models" part of the table, each line reports the results of a different model. The multiple binomial models do not include breeding success because data were available for only 2 of 3 study years (see Methods and Results). df, degrees of freedom; SE, standard error.

[a] *n* = 157.

[b] *n* = 155.

[c] *n* = 156.

[d] *n* = 93.

[e] *n* = 122.

[f] *n* = 123.

[g] *n* = 64.

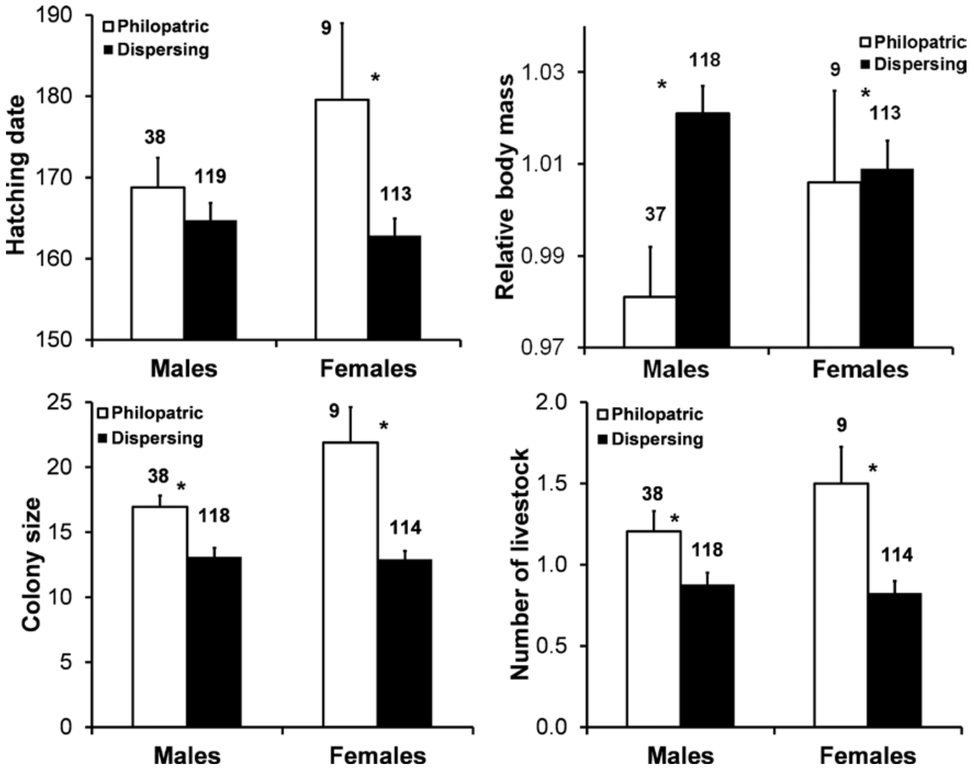

Figure 3

Graphs in first row: mean (+SE) hatching date (1 = 1 January) and body mass relative to the siblings for males and females that did (dispersing) or did not (philopatric) disperse. Second row: mean (+SE) colony size (number of pairs) and number of livestock ($\log_{10}$-transformed) at the colony of origin for males and females that did (dispersing) or did not (philopatric) disperse, as recorded in the year of recruitment. See also Methods.

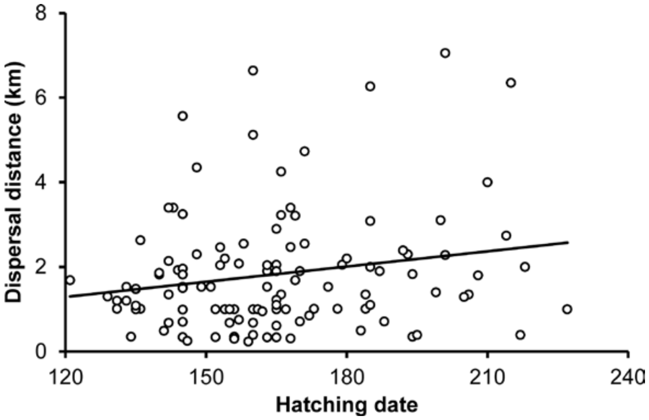

Figure 4

Relationship between dispersal distance of male offspring and hatching date (1 = 1 January).

Table 2

Multiple GLMM of dispersal distance in relation to sex, hatching date, and body mass of the recruit when nestling relative to its brood mates

	df	*F*	*P*
Sex	1,189	1.30	0.256
Hatching date	1,189	13.38	0.068
Relative body mass	1,189	4.78	0.030
Hatching date × Sex	1,189	6.34	0.013
Relative body mass × Sex	1,189	4.06	0.046
Relative body mass × Hatching date	1,189	3.25	0.073

Table 3

Binomial linear mixed models of dispersal propensity (philopatric = 0, dispersing = 1) of male offspring (n = 58) in relation to sex composition of their brood of origin

	Estimate (SE)	df	*F*	*P*
Number of male siblings	0.878 (0.768)	1,43	4.14	0.048
Number of female siblings	−0.073 (0.277)	1,43	0.07	0.792
Brood sex ratio	1.758 (1.080)	1,43	2.65	0.111

Each line reports the results of a different model.

DISCUSSION

We identified diverse factors that predict natal dispersal decisions of barn swallows. These factors operate in a reciprocally independent way, as suggested by the lack of statistically significant interaction effects. In addition, sex strongly affected both dispersal propensity and distance, with females being the most dispersing sex, as expected for our study species (Balbontín et al. 2009; Saino, Romano, Ambrosini, et al. 2012) and for birds in general (Greenwood and Harvey 1982; but see Schjørring 2001; Martín et al. 2008; Hardouin et al. 2012).

Context-dependent effects on dispersal

The negative effects of colony size and number of livestock at the colony site on dispersal were consistent with our predictions based on barn swallow population trends and habitat preferences (Møller 2001; Ambrosini et al. 2002; Turner 2006; Bani et al. 2009; Grüebler et al. 2010). Different additive mechanisms may have produced these associations. Livestock farming is a strong predictor of barn swallow breeding distribution (Møller 2001; Ambrosini et al. 2002, 2012; Grüebler et al. 2010). Colony size and livestock farming have large temporal autocorrelation and, as expected, the relationship between dispersal and colony size or livestock farming existed for both the year of recruitment and the year of birth. However, in multiple linear models, colony size retained its significant negative effect on dispersal, whereas the effect of livestock was no longer significant; this suggests that settling decisions may be more strongly dependent on colony size compared with livestock, indicating negative density-dependent dispersal propensity. To choose their settling colony, recruits could simply rely on personal information (Danchin et al. 2004) on habitat quality and food availability acquired as nestlings or after fledging before autumn migration (Reed et al. 1999; Danchin et al. 2001). Moreover, offspring may rely on inadvertent social information (Danchin et al. 2004; Nocera et al. 2006) on colony size in their natal year but also in the year of recruitment because yearlings arrive from migration later than adults (Saino et al. 2004), and the number of adults that have already settled at any given time when yearlings start to arrive from migration is proportional to overall colony size at the end of the breeding season (our personal observation). Access to social information on habitat quality, however, is unlikely to have occurred via observation of adults on parental duties or breeding success, as the latter did not predict dispersal (Serrano et al. 2004).

Natal dispersal of barn swallows has been previously shown to markedly vary among colonies (Balbontín et al. 2009), and present results therefore help in explaining the sources of variation in attractiveness of colony sites to dispersing young.

Ample correlational but also experimental evidence exists for an effect of habitat quality, including availability of resources (e.g., food), parasite infestation, or features relevant to the ecology of the particular species under scrutiny, on dispersal of birds (Kenward et al. 1993; Møller et al. 2004; Baglione et al. 2006; but see Nilsson 1990). Present results are, therefore, consistent with the general expectation of higher fidelity to a high-quality natal site. On the other hand, negative density dependence in dispersal that we observed in this study is relatively rare in birds, as positive density dependence is the prevailing pattern (see Matthysen 2005; Martín et al. 2008; Michler et al. 2011). The mechanisms that have been most frequently invoked as drivers of negative density-dependent dispersal, such as diminished individual risk of predation or enhanced foraging efficiency (Stamps 1988), are unlikely to operate in barn swallows. In fact, we could collect no evidence from our study population for any function of coloniality related to antipredator or foraging performance. In the barn swallow, negative density-dependent natal dispersal may be facilitated by downregulation of the population by density-independent effects acting during migration and wintering. These may cause breeding populations to be smaller than carrying capacity, and result in more offspring being recruited in larger colonies. Unsaturation of breeding habitat is suggested by the sharp population decline in southern Europe during the last decade (e.g., Bani et al. 2009; Ambrosini et al. 2012), possibly due to worsening ecological conditions during migration and wintering. It should be noted, however, that there was a hint for a weak positive density-dependent effect on dispersal propensity but only at the highest colony sizes, as suggested by polynomial regression of the proportion of philopatric individuals on colony size.

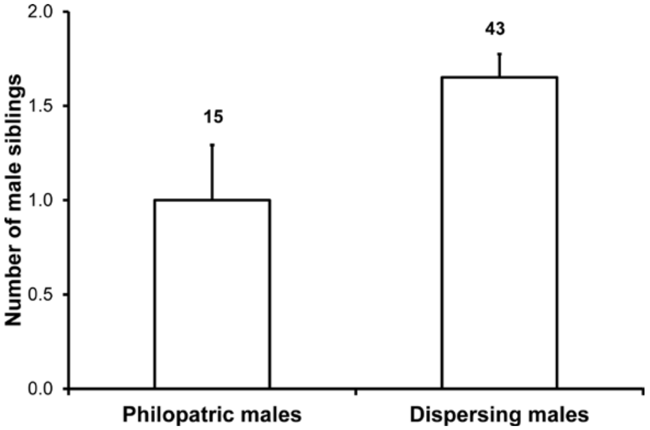

Figure 5
Mean (+SE) number of male siblings in the original brood of males that were recruited in their original colony or dispersed to another colony.

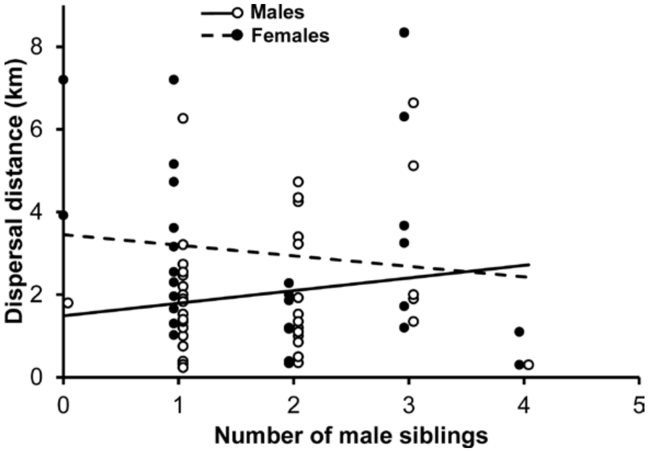

Figure 6
Dispersal distance of males or females that were recruited in a colony different from their original one in relation to the number of male siblings in their original brood.

Negative density dependence and habitat quality were similarly effective on dispersal of either sex, differently from what has been observed in some bird species where sex-specific effects have been detected (Matthysen 2005; Michler et al. 2011). Although the lack of statistically significant sex by context-dependent effects on dispersal propensity could partly arise because relatively small sample size of females reduced the statistical power of the tests, this evidence argues against a role of sexual selection in driving the response to context-dependent factors relevant to dispersal decisions.

Phenotype-dependent effect on dispersal

Differently from context-dependent factors, phenotype-dependent effects, including maternal effects mediated by hatching date, on dispersal were strongly differentiated between the sexes. Large males relative to their brood mates were more likely to disperse, whereas this was not the case for females. Conversely, females hatched late in the season were more likely to be philopatric, whereas no effect of hatching date on male dispersal was found. This picture is open to different interpretations.

In barn swallows, there is no obvious energetic cost of dispersal, dispersal distances being 3 or 4 orders of magnitude smaller than migration distances, but time and energy costs of prospection for suitable sites may be nonnegligible, and individuals in relatively good condition may be better at affording them. Indirect costs of dispersal may arise because of differences in local parasite fauna, whereby individuals ranking high in the brood hierarchy are better at coping with such parasite-mediated costs possibly because of their superior physiological state (see Boulinier et al. 2001; Tschirren et al. 2007; Bonte et al. 2012). The present results may, thus, suggest that ranking high in the brood hierarchy alleviates any prospection or indirect costs of dispersal more for males than for females. Although long-term effects of position in the brood size hierarchy may seem puzzling, this variable has been shown to predict life expectancy after sexual maturity in barn swallows, suggesting that it has carryover effects until adulthood possibly via nutritional determinisms of growth and maturation of bodily functions such as immunity (Saino, Romano, Ambrosini, et al. 2012). Position in the brood hierarchy depends on position of the original egg in the laying sequence (Ferrari et al. 2006; our unpublished results). An alternative interpretation for the association between dispersal propensity and relative body mass is, therefore, that differences in dispersal reflect developmentally entrenched maternal effects via egg quality (Tschirren et al. 2007). Maternal hormones have major organizational effects (Groothuis et al. 2005). Variation in steroid hormone profiles (androgens and glucocorticoids) is known to explain variation in dispersal (see Dufty and Belthoff 2001). Egg hormone concentrations may vary according to egg-laying order (e.g., Groothuis et al. 2005; Rubolini et al. 2011), as it has also been observed in a nearby Italian barn swallow population where androstenedione concentration significantly decreased with laying order (our unpublished results). Thus, the association between relative body mass and dispersal may depend on long-term organizational effects of maternal egg hormones (see also Altwegg et al. 2000). However, it must be emphasized that the adaptive value of any such dependency of male dispersal propensity on laying order is unknown, and might simply arise as a side effect of within-clutch variation in egg composition, which evolves under functionally different selection pressures for strategic allocation of maternal effects. The fact that the association between relative body mass, as a proxy for laying order, and dispersal propensity was not observed among females (see also Altwegg et al. 2000) could be explained by sex-related susceptibility to the organizational effects of egg androgens (see Saino et al. 2006; but see Tschirren et al. 2007).

The sex-related effect of relative body mass on dispersal distance was different from that on dispersal propensity: relatively large females dispersed over larger distances, whereas dispersal distance of males was independent of relative body mass. This effect could arise if prospection for a place to disperse depends on body condition at fledging and occurs already during premigratory dispersal. Females ranking high in their brood mass hierarchy could be better at prospecting if, for example, prospecting competes with important activities like foraging (see also above). Because of disproportionate increase in the number of farms with increasing distance from the natal colony, relatively high-quality colonies are more likely to be found as distance from the natal colony increases. High-ranking females would, therefore, be more likely to end up in a relatively distant colony. Alternatively, laying-order effects mediated by egg hormones could operate. Obviously, this interpretation leaves the question of why no relation between dispersal distance and body mass rank was observed in males unresolved, and we have no explanation for this, except that smaller average dispersal distances of males reduce the costs of prospection and may therefore result in a weaker, hardly detectable association with body condition.

Sex-dependent variation in the association between dispersal distance and indicators of body condition has also been uncovered in other studies of birds, although which sex was more affected by body condition and the sign of the association between dispersal and body condition again varied among species (e.g., Tilgar et al. 2010; Hardouin et al. 2012). Moreover, in other studies, no effect of nestling body mass on dispersal could be identified (Verhulst et al. 1997).

Maternal effects translated into differential dispersal of females, but not males, via hatching date. Late-hatched females were less prone to disperse than early-hatched ones. However, dispersal distance was positively predicted by hatching date in males, whereas this relationship was nonsignificant among females. Philopatry of late-hatched females may be due to seasonal effects on postnatal prospection for suitable breeding sites during the first summer or on return from first migration, if hatching date carries over on arrival date. Alternatively, this could represent the effect of deterioration of any aspect of body condition that affects dispersal and declines along the breeding season. The positive effect of hatching date on dispersal distance of males and the lack of effect on dispersal per se remain puzzling. Male marsh tits (*Parus palustris*), for example, have also been shown to disperse farther when hatched late (Nilsson 1989; see also Pärt 1990), but the social mechanisms controlling dispersal in that resident, all-purpose territorial species can hardly be extended to the barn swallow. The effect of hatching date on dispersal has not been found in other bird studies (e.g., Verhulst et al. 1997).

Overall, the present results on dispersal propensity and dispersal distance in relation to relative body mass or hatching date in either sex, thus, suggest that in barn swallows the decisions of whether to disperse and of dispersal distance appear to be different processes that are controlled in different ways by the same traits (see also Stevens et al. 2012; Baguette et al. 2013) and these traits act in a markedly sex-specific way. Notably, no interaction effects among context- and phenotype-dependent effects on dispersal decisions existed. Hence, we could uncover no individual state-dependent response to context-dependent factors or variation in density dependence of dispersal according to habitat quality, differently from other studies (Verhulst et al. 1997; Pärn et al. 2012).

Kin-dependent effects on dispersal

Sex composition of the brood was expected to act in a different way on dispersal decisions of the 2 sexes. Indeed, because of the relatively small size of barn swallow colonies (mean number of pairs 4.8–5.7 from a random sample of farms from a nearby population; Sicurella et al. 2013), the short dispersal distance of males, and the male-biased sex ratio among adults (Møller 1994; Saino et al. 2013), the risk of local competition between male siblings is nonnegligible. Consistently with our prediction, we found that both dispersal propensity and distance of male offspring increased with the number of male siblings. Conversely, neither variable was predicted by the number of female siblings. This was expected because large dispersal distance of females should reduce the risk of inbreeding. It is important to note that philopatric males incur low risk of inbreeding with their mothers because partial temporal segregation in arrival and breeding dates exists between yearlings and older individuals (Saino et al. 2004; Saino, Romano, Caprioli, et al. 2012), and the chances that 2- or more-year-old philopatric male recruits mate with their 3- or more-year-old mothers are further reduced by low annual survival rates. Thus, this study adds to the scant empirical evidence that the sex composition of the original brood has an effect on dispersal decisions, possibly via the effect of competition for mates (see Pasinelli and Walters 2002). Because male–male competition for mates is exacerbated in male-biased populations, this finding complements the observation that local population-level sex ratio in the year of settling can be an important component of dispersal and settling decisions as shown in experiments (Nicolaus et al. 2012) and in a correlational study of the barn swallow (Saino et al. 2013). In a previous study of different barn swallow populations, no evidence was found that dispersal depended on the expression of secondary sexual characters or body condition measured on adult recruits (Balbontín et al. 2009).

In conclusion, we showed that diverse, context-dependent factors (colony size and livestock farming) and maternal or phenotype-dependent effects (sex, hatching date, and position in the brood body mass/laying-order hierarchy) affect the natal dispersal decisions of barn swallows. Deciding if dispersing or not and decisions on dispersal distance seem to be separate processes, which are at least partly controlled by different factors. This is consistent with patterns of decoupling of dispersal propensity and dispersal distance observed in other taxa (Stevens et al. 2012; Baguette et al. 2013). Both dispersal per se and dispersal distance of males are predicted by the number of male siblings in the brood of origin, likely because kin selection favors males that reduce the risk of competing for mates with kin in a population with male-biased tertiary sex ratio. In general, patterns of association of natal dispersal propensity and distance with context-, phenotype- and kin-dependent factors, including those that we described here, broadly vary among species. Although natal dispersal studies are typically hampered by practical difficulties, greater effort is needed to expand our knowledge on the proximate mechanisms controlling natal dispersal in different species and to identify the causes of among-species and population differences in such mechanisms.

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Chapter 4

Brothers and sisters are stabbing each other in the back: long-term effects of sex of siblings on barn swallow offspring

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Brothers and sisters are stabbing each other in the back: long-term effects of sex of siblings on barn swallow offspring

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Prenatal and early postnatal conditions can prime developmental trajectories, with short- as well as major long-term effects on phenotype. Variance in perinatal conditions may be caused by many factors, including number of siblings of either sex, which is expected to influence individual phenotype for two complementary reasons. First, male and female offspring can differ in susceptibility to extrinsic conditions. Second, the effect that an individual has on its siblings can differ according to their sex. Yet, few studies of vertebrates and only one of birds have addressed the long-term consequences of family sex composition on offspring of either sex. We analysed the effect of brood sex composition on adult phenotype and breeding performance in the barn swallow, *Hirundo rustica*. Male offspring growing with more sisters had shorter wing length, an aerodynamically important trait, and tail length, a condition-dependent, sexually selected trait. In addition, tail length of females decreased with increasing brood size but more steeply so when they grew with more female siblings. Body size of females also declined with increasing brood size. Notably, breeding output of females declined with an increasing proportion of male siblings and also with increasing brood size. This study thus suggests that social environment has major consequences for phenotype and breeding performance in adulthood and that variation in brood sex composition has long-term effects which depend on the sex of the individual as well as on the specific trait considered. Hence, optimal parental sex allocation decisions depend not simply on additive fitness costs and benefits of producing males or females, but also on the long-term effects that sons and daughters exert on each other.

Phenotypic variation in populations of organisms arises partly as the expression of norms of reaction to the extrinsic factors to which individuals are exposed early in life (Schlichting & Pigliucci, 1998). The flow of causation between the conditions that individuals experience during the pre- or early postnatal stages and performance later in life has been dissected in a number of animal and plant models (Lindström, 1999; Metcalfe & Monaghan, 2001 Mousseau & Fox, 1998). The studies of such carryover effects have hinted at long-term effects that are eventually expressed after sexual maturation, potentially being as important in determining individual fitness as are short-term effects (Cam, Monnat, & Hines, 2003; van de Pol, Bruinzeel, Heg, van der Jeugd, & Verhulst, 2006).

In essence, so called ‘silver spoon’ (Grafen, 1988) effects of early life conditions, whereby maternal effects or rearing environment may have life-long consequences on performance, depend on three, tightly linked processes. First, variation in parental quality contributes to setting the environmental scene for the growing offspring. High-quality parents can secure favourable conditions with ‘developmentally entrenched’ effects, possibly mediated by egg quality or by pre- or postnatal care (Badyaev, 2008; Cam & Aubry, 2011; Carere & Balthazart, 2007; Groothuis & Schwabl, 2008; Mousseau & Fox, 1998; Ruuskanen, Doligez, Pitala, Gustafsson, & Laaksonen, 2012). Second, habitat quality can add to variation in the extrinsic conditions experienced by the offspring via, for example, effects of nutritional conditions (Metcalfe & Monaghan, 2001; van de Pol et al., 2006; Sergio et al., 2009). Parental and environmental quality are likely to covary positively and, by acting independently or in concert, can have long-term consequences for fitness traits of mature offspring as diverse as development of ‘ordinary’ and secondary sexual characters (Gustafsson, Qvarnström, & Sheldon, 1995; de Kogel, 1997; de Kogel & Prijs, 1996; Nowicki, Peters, & Podos, 1998), dispersal (Nicolaus

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et al., 2012), viability or recruitment (Cam et al., 2003; Potti, 1999a, 1999b), offspring number and quality (Cam et al., 2003; van de Pol et al., 2006; Potti, 1999b) or breeding habitat quality (Verhulst, Perrins, & Riddington, 1997; see also Cam & Aubry, 2011; Tilgar, Mänd, Kilgas, & Mägi, 2010). The intimate connection between parental and environmental effects (see Sergio et al., 2009) is exemplified by seasonal effects. In spatially heterogeneous, seasonally varying temperate habitats, low-quality individuals may settle in poor-quality habitats (Rodenhouse, Sherry, & Holmes, 1997) and fail to achieve reproductive state at the time when conditions for breeding are optimal. Under such circumstances, the frequently observed negative covariation between offspring quality/viability and birth date (e.g. Naef-Daenzer, Widmer, & Nuber, 2001; Saino et al., 2012; Verboven & Visser, 1998) may be ultimately caused by the concomitant effects of habitat and parental quality on breeding date.

Third, social environment, and interactions with competing kin in particular, can produce huge variation in offspring growth trajectories and general physiological state at the within-family level (Mock & Parker, 1997; Wright & Leonard, 2002), with immediate but also persistent consequences for morphological and physiological traits, and thus for survival and/or reproductive success (Lindström, 1999). A potentially major determinant of the long-term outcome of interactions between siblings that has remained neglected is sex, despite straightforward molecular sexing techniques having been devised many years ago. Yet, there are two compelling, complementary reasons to expect that the number of male or female siblings sharing a rearing environment can influence the long-term fitness consequences of sibling competitive interactions. First, asymmetries often occur between male and female siblings in competitive interactions over limiting resources (see Uller, 2006). These can result from a variety of proximate causes including intersexual variation in social behaviour which is established early in life, differences in resource demands or size-related dominance in species with early established sexual dimorphism, or parental favouritism for either sex (e.g. Badyaev, 2002; Bonisoli-Alquati, Boncoraglio, Caprioli, & Saino, 2011; Lessells, 2002; Saino et al., 2010; Uller, 2006). Second, young of either sex may differ in their susceptibility to the same features of their rearing habitat, whereby competition over limiting parental resources with any given offspring can have different effects on male or female siblings (Bonisoli-Alquati et al., 2011; Gustafsson, 1989; Lindström, 1999; Oddie, 2000; Uller, 2006).

Short-term sex-dependent competitive behaviour and its consequences for growth and survival before independence have been investigated in some studies of altricial birds (Boncoraglio, Martinelli, & Saino, 2008; Saino, de Ayala, Martinelli, & Boncoraglio, 2008; Uller 2006). However, few studies exist on the consequences of family sex composition for phenotype and performance in adulthood in vertebrates in general (Uller, 2006) and, to our knowledge, only one of them has concerned birds (Radersma, 2011). Yet, such studies are expected to shed more light on, and potentially also add a further level of complexity to, the analysis of the evolution of reproductive strategies and of sex allocation decisions in particular.

In the present study we thus used a small passerine bird, the barn swallow, *Hirundo rustica*, as a model to investigate the effects that brood sex composition and brood size have on morphology and seasonal breeding success of the offspring that were eventually recruited into the study population as breeding adults.

In the barn swallow, male offspring are penalized more than females by adverse rearing conditions and when they compete with female compared to male siblings (Bonisoli-Alquati et al., 2011; Saino, de Ayala, et al., 2008; see also Boncoraglio et al., 2008). Average nestling phenotypic quality declines with brood size (Saino, Calza, & Møller, 1997; Saino et al., 2000). In addition, hatching date negatively predicts life expectancy after sexual maturation and lifetime reproductive output, implying that early maternal effects and postnatal conditions and/or parental quality have major consequences for viability and fecundity (Saino et al., 2012). While the studies of barn swallows to date have focused on the effects of brood sex composition on growth and general state during the nestling period, no study has been carried out on the consequences of brood sex composition in adulthood. We predicted that phenotypic values of traits that reflect growth (keel length), body condition (adult body mass, plumage growth and ornamental tail length; Møller, 1994) and breeding performance would decrease, and particularly so among males, with an increasing proportion of female siblings. Generally negative associations between phenotypic values or breeding performance and brood size were also expected irrespective of fledgling sex. Because hatching date may affect adult performance (Saino et al., 2012), in the analyses we controlled for the effect of hatching date. In addition, because the effect of hatching date on performance may be partly mediated by the order (first or later) of the clutch of origin, in the analyses we also controlled for this potentially confounding effect.

METHODS

Study Organism

The barn swallow is a small (ca. 20 g), insectivorous, long-distance migratory passerine (Møller, 1994; Turner, 2006). Breeding typically occurs in colonies of two to tens of pairs, inside rural buildings such as cowsheds (Møller, 1994; Turner, 2006). Socially monogamous pairs have one to three clutches of two to seven eggs per breeding season. Hatching asynchrony is small (hatching spread: 24–36 h), with first-laid eggs hatching first (Saino, Incagli, Martinelli, Ambrosini, & Møller, 2001). Altricial nestlings fledge when ca. 18–20 days old. The single annual moult of rectrix (tail) and remex (wing) feathers occurs during wintering in Africa (Ginn & Melville, 1983). Sexual dimorphism in size is small, but males have longer wing and tail feathers (Møller, de Lope, & Saino, 1995).

Field Methods

In spring–summer 2010–2012 we studied 38 barn swallow colonies (=farms) in the Magadino Plain (southern Switzerland, barycentre of the study farms: 46°9′54″N, 8°55′47″E). The study area (10 × 4 km) mainly consists of farmland and is dominated by maize and hay fields. In 2010 and 2011 we visited the nests every 10–12 days to record breeding events, ring the nestlings ($N = 1248$ in 2010 and 1353 in 2011), and collect a small blood sample by puncturing the ulnar vein for molecular sexing (Saino, Martinelli, & Romano, 2008). Hatching date could be either directly identified upon nest inspection or estimated according to several cues (e.g. chick feathering; see Ambrosini & Saino, 2010).

We intensively captured the adults at the colonies in 2011 and 2012 by placing mist nests before dawn at the exits of the rural buildings in which breeding individuals usually spend the night. Upon capture we identified the recruits and measured body mass, keel length (a proxy for body size), the length of the longest (ninth) primary wing feather (a proxy for wing length) and the length of the left outermost tail feather (a sexually selected trait in males; Møller, 1994). Recruits were colour-ringed to assign them to breeding pairs and to identify their nests, which were regularly inspected to record the size of the clutches and breeding output (number of nestlings at last visit). Total numbers of eggs and fledglings were used as indicators of seasonal fecundity and breeding output, respectively. The sample included 87 recruits from 76 broods with a total of 361 nestlings; for all but four nestlings we could identify the sex by molecular tools (Saino, Martinelli, et al., 2008). Among the 87 recruits, 72% were from first broods while the remainder were from second or third broods. For six recruits, measurements were available from their second year after hatching while for the other recruits measurements were taken in the first year after hatching. Controlling for actual year at measurement in the analyses did not change the results (see Statistical Analyses).

In the present correlational study, we did not attempt an experimental approach by manipulating brood sex composition, for the following reasons: (1) manipulating brood sex composition requires identifying pairs of synchronous broods (i.e. broods hatching on the same day) preferably from the same colony. However, synchronous broods are relatively rare, particularly in our declining study populations; (2) large natal dispersal and post-fledging mortality result in very few barn swallow offspring being recruited as adults in their breeding colony (Møller, 1994; Turner, 2006), implying that a very large number of manipulated broods would be required to obtain a reasonably large sample of recruits; manipulating such a large number of broods would require extremely demanding effort in fieldwork and a large study area; (3) to manipulate the brood sex composition in a way that effectively alters the ‘nest sex environment’ from the very early nestling stage, manipulation should have occurred soon after hatching. However, collecting blood a few days after hatching may harm the nestlings and performing molecular sexing while also working in the field poses technical and logistic difficulties. Conversely, in the present study inclusion of the broods in the sample was not constrained by synchrony with other broods, blood sampling could be done at an age when it is known not to harm the nestlings and molecular sexing could be run after the field season.

The study was carried out with the approval of the Office fédéral de l’environnement OFEV, Division Espèces, écosystèmes, paysages (F044-0799).

Statistical Analyses

We analysed morphological traits and breeding variables of recruits recorded in the season of recruitment in relation to sex (factor), sex ratio of the siblings (proportion of males among the siblings of the individual recruit, computed while excluding the individual recruit itself; hereafter ‘sibling sex ratio’), brood size (number of nestlings in the brood) and hatching date (covariates) in linear mixed models (LMM) including colony, year of birth and nest of origin as random factors. In all models, a normal error distribution and an identity link function was assumed. The analyses were first run on the two sexes separately and then on the two sexes pooled to test for any sex by sibling sex ratio or brood size interaction effects. Because likelihood ratio tests showed that the random effects of colony and year of birth never contributed significantly to the fit of the models ($\chi^2_2 < 4.90$, $P > 0.05$ in all cases), these random effects were always excluded. However, in all models of variables for which pairs of sibling recruits were included, brood of origin was retained as a random effect. In statistical tests of fixed effects the denominator degrees of freedom were conservatively assumed to equal the number of broods of origin. Because no pairs of siblings were included in the sample for which information on annual clutch size and breeding output was available, these data were analysed in linear models.

Hatching date and brood order (first or second brood) are strongly positively correlated ($r > 0.70$ for recruits of both sexes) and could therefore not be entered simultaneously as predictors in the models. Based on previous evidence, we expected hatching date to affect offspring performance. We therefore first tested for any effect of brood order on the phenotypic variables while controlling for the effect of sibling sex ratio and brood size. As we found no significant effect of brood order (F values were associated with P values > 0.10), in the remainder of the paper we present only the analyses including the effect of hatching date. Six of the 87 individual recruits were measured in their second year after hatching (see also above). Including a fixed-effect factor accounting for age at measurement did not qualitatively change the results, that is, the significant and the nonsignificant effects of sibling sex ratio and brood size remained such in models that either included or excluded the effect of age at measurement. For simplicity, we therefore present the results of the analyses excluding the effect of age.

We also ran LMM or linear models of phenotypic and breeding performance variables by including the absolute number of male or female siblings as predictors, rather than sibling sex ratio, because the effect of offspring of either sex on their siblings might be considered to depend on absolute rather than relative number of offspring of either sex.

In the text, estimated parameters are presented with their associated SE in parentheses. All the analyses were run using SAS 9.2 (SAS Institute Inc., Cary, NC, U.S.A.) and SPSS13 (SPSS Inc., Upper Saddle River, NJ, U.S.A.).

RESULTS

Adult Morphology and Brood Sex Composition

Body mass of male and female recruits was not significantly predicted by sibling sex ratio or brood size (Table 1). This result was confirmed in LMMs in which we controlled for the effect of hatching date of recruits, and also for date at body mass measurement, because body mass may vary seasonally (details not shown).

Keel length of male recruits was not significantly predicted by the proportion of siblings that were male in the original brood after we controlled for the effect of brood size, nor by brood size itself (Table 1). Keel length of females, however, was negatively predicted by brood size, after we controlled for sibling sex ratio (Table 1, Fig. 1). Wing length of male recruits increased significantly with an increasing proportion of male siblings when we controlled for brood size, whereas wing length of females was not predicted by sibling sex ratio or brood size (Table 1, Fig. 2). Tail length was not predicted by brood size or sex ratio in either sex (Table 1). The effect of the interaction between sibling sex ratio and brood size on the traits in Table 1 was never found to be significant, except for tail length of females ($F_{1,30} = 5.20$, $P = 0.030$). The coefficients of the model (sibling sex ratio: −464.61 (221.90); brood size: −97.33 (42.39); interaction: 112.95 (49.55)) indicate that female tail length declined with increasing brood size but this decline was steeper for female recruits with relatively more female siblings.

In LMMs on the two sexes pooled with sibling sex ratio, brood size, sex and their two-way interactions, we found a significant brood size*sex interaction effect on keel length ($F_{1,76} = 5.04$, $P = 0.028$; coefficient for males: −6.04 (19.18); females: −47.54(22.56)), and a significant sibling sex ratio*sex interaction effect on wing length ($F_{1,76} = 7.55$, $P = 0.008$; coefficient for males: 18.59 (33.33); females: −36.53 (34.99)), indicating that the slope of these relations differed between male and female recruits. However, in these models the other two-way interactions did not attain significance. Similar models of body mass or tail length did not disclose any significant interaction effects among sibling sex ratio, brood size and sex (details not shown).

When we included the effect of hatching date in the models in Table 1, the results remained qualitatively unchanged, that is, all the significant effects reported in Table 1 remained such. In addition, there was no significant effect of hatching date per se on any

Table 1
Morphological variables of male and female recruits in relation to sex ratio (proportion of males among their siblings) and brood size

	Males					Females				
	F	*df*	*n,N*	*P*	Coefficient (SE)	*F*	*df*	*n,N*	*P*	Coefficient (SE)
Body mass										
Sex ratio	0.81	1,51	53,51	0.373	5.54 (6.16)	0.15	1,32	33,32	0.704	−4.19 (10.94)
Brood size	0.00	1,51		0.948	−0.12 (1.83)	0.03	1,32		0.875	0.50 (3.15)
Keel length										
Sex ratio	3.56	1,52	54,52	0.065	79.57 (42.17)	0.20	1,31	32,31	0.661	19.03 (42.95)
Brood size	0.08	1,52		0.782	3.47 (12.47)	13.63	1,31		0.001	−45.17 (12.23)
Wing length										
Sex ratio	10.48	1,52	54,52	0.002	42.21 (13.04)	1.10	1,32	33,32	0.303	−15.19 (14.50)
Brood size	1.04	1,52		0.314	3.91 (3.84)	0.08	1,32		0.782	−1.17 (4.18)
Tail length										
Sex ratio	0.03	1,50	52,50	0.868	−4.74 (28.23)	0.41	1,30	31,30	0.528	30.60 (47.95)
Brood size	1.32	1,50		0.257	−9.93 (8.66)	0.14	1,30		0.708	−5.32 (14.06)
Seasonal number of eggs										
Sex ratio	0.06	1,12	15,15	0.817	0.57 (2.43)	4.00	1,13	16,16	0.067	−3.13 (1.56)
Brood size	0.12	1,12		0.737	0.31 (0.91)	13.00	1,13		0.003	−1.60 (0.44)
Seasonal breeding success										
Sex ratio	1.29	1,14	17,17	0.275	2.72 (2.39)	7.13	1,14	17,17	0.018	−4.48 (1.68)
Brood size	0.01	1,14		0.934	0.07 (0.84)	9.00	1,14		0.010	−1.43 (0.48)

In the linear models of morphological traits, we included the random effect of nest of origin (see Statistical analyses).
n,N: number of recruits, number of nests of origin from which the recruits originated. Denominator degrees of freedom are set equal to the number of nests of origin.

morphological variable (*F* values were associated with *P* values > 0.09; other details not shown).

The results of the LMMs of recruit morphology with nest of origin as a random factor and the absolute number of siblings of either sex (see Statistical Analyses) and hatching date as independent variables were consistent with the results presented in Table 1. In addition, these models disclosed a significant negative effect of the absolute number of female siblings on tail length of male recruits ($F_{1,50} = 5.27$, $P = 0.026$; coefficient: −19.25 (8.38); Fig. 3).

Seasonal Breeding Performance and Brood Sex Composition

In linear models, the seasonal number of eggs laid declined significantly with increasing size of the original brood of the female recruits (Table 1). For female recruits, the total number of offspring produced during the breeding season also declined significantly with increasing proportion of male siblings and with increasing natal brood size (Table 1, Fig. 4). On the other hand, breeding performance of males did not covary with natal brood size or sibling sex ratio. Linear models of female data including hatching date as a covariate confirmed the negative effect of natal brood size on the number of eggs laid ($F_{1,12} = 12.08$, $P = 0.005$; coefficient: −1.59 (0.46)) and on seasonal breeding output ($F_{1,13} = 8.42$, $P = 0.012$; coefficient: −1.42 (0.49)), as well as the negative effect of sibling sex ratio ($F_{1,13} = 6.23$, $P = 0.027$; coefficient: −4.36 (1.75)) on seasonal breeding output (see Table 1 for sample sizes). These linear models did not disclose any significant effect of hatching date per se (*F* values were associated with *P* values > 0.64; other details not shown).

Linear models with absolute number of brothers or sisters as predictors showed that both total number of eggs and seasonal breeding output of females declined with increasing number of male siblings (effect on number of eggs: $F_{1,12} = 11.18$, $P = 0.005$; coefficient: −1.71 (0.51); seasonal breeding output: $F_{1,14} = 12.29$, $P = 0.003$; coefficient: −1.75 (0.50)).

For breeding performance variables we refrained from analysing the differential effects of sex ratio or brood size on male and female recruits in models with interaction terms owing to the constraint of sample size on statistical power of the tests.

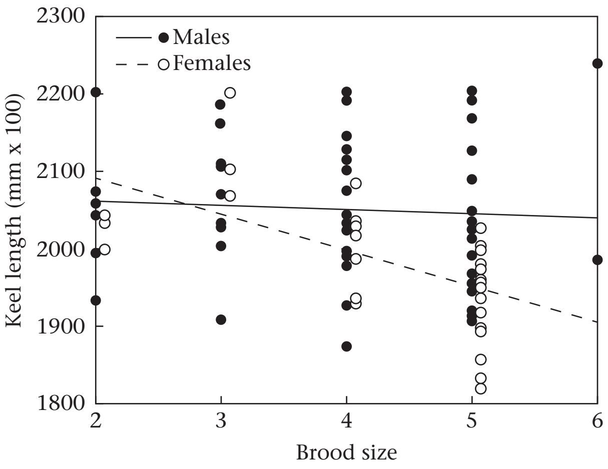

Figure 1. Keel length (a proxy of body size) of recruits in relation to original brood size.

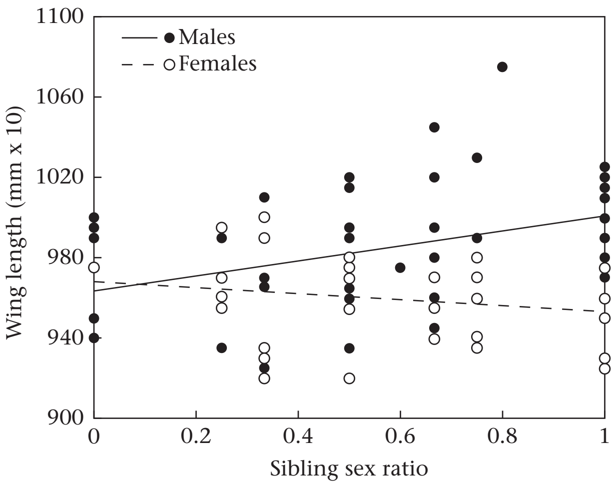

Figure 2. Wing length (indexed by length of the ninth primary wing feather) of male and female recruits in relation to the proportion of males among their siblings.

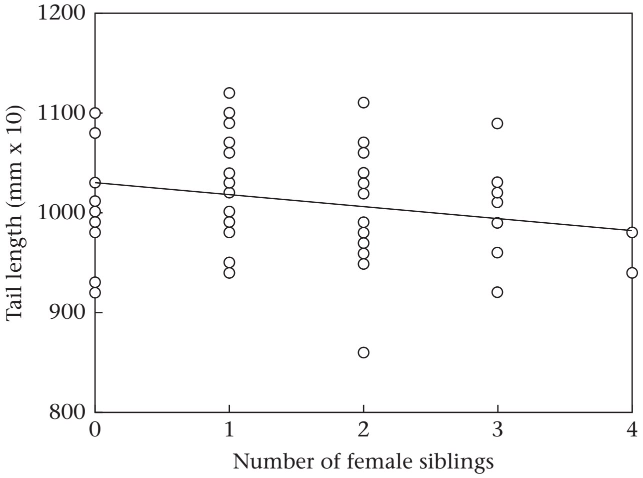

Figure 3. Tail length of male recruits in relation to the absolute number of females among their siblings (see Results). Including the second-order polynomial term of the number of female siblings in the model did not significantly improve the fit of the model.

DISCUSSION

We analysed the long-term effects of sex composition and size of the brood of origin on morphological traits and seasonal reproductive output of adult barn swallows. Morphology and breeding performance of male and female offspring were differentially affected by the proportion of siblings that were male. This study thus supports the conclusions of the only other study of birds of which we are aware, which found carryover effects of brood sex composition on major fitness traits expressed in adulthood (Radersma, 2011). Moreover, we found that specific phenotypic values of adults and breeding performance of females declined with increasing size of the brood of origin.

Consistently with our prediction, males with relatively more sisters suffered negative effects in terms of wing length, suggesting that a large proportion of female nestlings creates an unfavourable nest environment for their brothers. Because feathers are moulted during the first winter in Africa, the negative effects of a large proportion of female siblings were expressed in the long term and affected a crucial physiological activity, plumage moult, which can have important repercussions on flight performance of this long-distance migratory bird.

Length of the outermost tail feathers of males, which is a condition-dependent trait under intersexual selection (Møller, 1994; Møller et al., 2006; Turner, 2006) did not covary with the proportion of brothers but covaried negatively with the absolute number of sisters. This puzzling evidence, that the absolute but not the relative number of sisters negatively predicted tail length of male siblings, is open to different interpretations. For example, in dyadic tests, males competing with a male sibling were found to gain more mass than when competing with a female sibling (Bonisoli-Alquati et al., 2011), suggesting that a large number of sisters may result in poorer nutritional conditions for males when nestlings, with carryover effects into adulthood (see also below). Rearing conditions, including stress and nutrition, have been shown to affect development of sexually selected traits later in life (Nowicki, Hasselquist, Bensch, & Peters, 2000; Nowicki et al., 1998; Ohlsson, Smith, Råberg, & Hasselquist, 2002). Our present results therefore suggest that sibling sex may be an ultimate source of variation in rearing conditions with consequences for the expression of sexual ornaments in adulthood. We also unexpectedly found that tail length of females decreased with increasing brood size but this negative effect of brood size was more pronounced for female recruits with relatively more sisters. This finding suggests that tail length of females may also be influenced by the nest sex environment, potentially serving as a clue to rearing conditions and thus phenotypic quality in sexual communication (Møller, 1994).

A striking finding of our study was the negative statistical effect of an increasing proportion (and absolute number) of males on breeding output of their female siblings. The intensity of this effect was non-negligible. Modal brood size of yearling barn swallows was four. An increase by 0.33 in the proportion of male siblings (corresponding to one additional male among three siblings) can be estimated (see Table 1) to cause a reduction of seasonal reproductive output of ca. 1.5 offspring, which equals approximately 25% of seasonal reproductive output of an average yearling. The mechanisms that mediate any causal link between the proportion of male siblings and breeding performance of females are a matter of speculation. Previous evidence suggests that a male-biased brood sex ratio has negative consequences for growth of both male and female barn swallows (Saino, de Ayala, et al., 2008). This effect may arise because of larger nutritional demands by male offspring and/or because males are more competitive and therefore create a more stressful environment for the entire brood (see Boncoraglio et al. 2008; Saino, de Ayala, et al., 2008). These effects would be unrelated to sexual size dimorphism at the nestling stage, which has been shown to be minimal in the barn swallow (Saino, Ambrosini, et al., 2002; Saino, de Ayala, et al., 2008). Hence, our results provide evidence that carryover effects of rearing conditions on female fecundity in birds (see Mainwaring, Blount, & Hartley, 2012; Sedinger, Flint, & Linberg, 1995) may depend on sibling sex.

Independently of which mechanisms are involved in generating these sex-dependent effects on breeding performance, the present results have important implications for the study of the evolution of reproductive strategies. Sex allocation theory predicts that investment in male and female offspring should be adjusted according to the fitness rewards that parents accrue from the production of either sex (Roulin, Altwegg, Jensen, Steinsland, & Schaub, 2010; Trivers & Willard, 1973; West, Herre, & Sheldon, 2000). The specific fitness costs and benefits of producing individual sons or daughters may depend on environmental conditions (Benito & Gonzáles-Solís, 2007). Our findings imply, however, that the overall parental fitness payoff of producing sons or daughters is not a

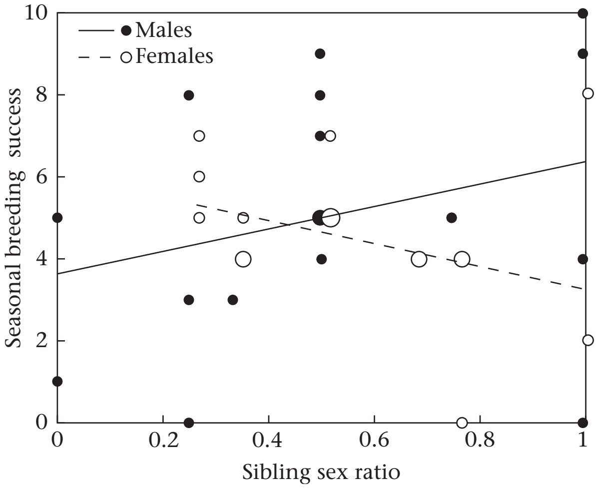

Figure 4. Seasonal breeding success (total number of fledglings produced by male and female recruits during the whole breeding season) in relation to the proportion of males among their siblings. Data points for females are slightly shifted to the right to avoid overlap with data points for males. Small, medium-sized or large symbols indicate one, two or three overlapping data points, respectively.

simple, additive function of the number of sons or daughters, because sons and daughters differentially affect the phenotype and performance of their sisters or brothers. Optimization of sex allocation will therefore depend not only on the balance between the reproductive value and the cost of producing individual offspring of either sex, but also on the effect that any offspring have on the reproductive value of the opposite sex (Uller, 2006). In the case of barn swallows, it appears that male and female offspring have reciprocal, negative and trait-specific effects on the opposite sex, targeting functionally important morphological traits (males) and reproductive performance (females), in a sex-specific way. Such reciprocal effects between the sexes may be expected to select for the production of progeny with nonrandom sex assortment. In particular, owing to reciprocal negative effects between the sexes, an excess of unisexual broods may be expected to occur. However, preliminary analyses on a large data set of brood sex ratios from the same population in which the present study was carried out have failed to find any marked deviation from random sex composition (our unpublished data; but see Saino, Ambrosini, et al., 2002).

Because of the correlative nature of the study, we carefully scrutinized our findings for potentially alternative interpretations. In general, it could be speculated that allocation strategies, rather than the reciprocal, direct effects of male and female nestlings, could produce the covariation between number of nestlings of either sex and phenotypic values of the opposite sex. If different breeding pairs differentially invest in either sex, they could do so both by producing more of the preferred sex and by preferentially allocating beneficial maternal effects/care to that sex. A slightly different possibility is that mothers and/or fathers preferentially care for offspring of their own or of the opposite sex (Lessells, 2002), and that the two parents differ in parental performance. If this is the case, offspring of either sex may be both more numerous, as an effect of better survival in the nest, and in better condition. While these interpretations are theoretically tenable, we are convinced that the existing evidence argues against at least some of them. In fact, in studies of the barn swallow we found no evidence of differential postnatal allocation to sex (Saino, Ellegren, & Møller, 1999; our unpublished results). In addition, survival rate up to the fledging stage is very high, suggesting that the scope for post-hatching variation in brood sex ratio from mortality is very limited (Boncoraglio, Caprioli, & Saino, 2009).

An alternative interpretation is that the numerically prevailing sex can prime the type of care (e.g. food quality) that is provided to the entire brood by, for example, influencing parental foraging behaviour. This could translate into suboptimal parental care for the rarer sex and thus into declining phenotypic values with increasing number of offspring of the opposite sex. At present, we have no empirical data to test this alternative.

Besides sex-specific effects of the proportion of brothers and sisters, we also uncovered short- as well as long-term effects of brood size. In particular, body size and seasonal breeding output of females and tail length of male recruits declined with increasing brood size. Negative effects of brood size were expected, as it has been repeatedly shown that the phenotypic quality of nestlings declines with increasing brood size, probably because of competition and increased per capita ectoparasite load (Saino et al., 1997; Saino, Ferrari, Romano, Ambrosini, & Møller, 2002).

Contrary to our expectation, phenotypic values in the present sample were not predicted by hatching date. Early-hatched nestlings of both sexes enjoy greater lifetime reproductive output and longevity after sexual maturation (Saino et al., 2012). The flow of causation between hatching date and lifetime fitness remains to be elucidated. Yet, the present study suggests that the effect of hatching date on lifetime fitness is not mediated by the phenotypic traits that we considered here.

In conclusion, this study provides evidence for reciprocal negative effects between offspring of either sex on functionally important morphological traits as well as on breeding output that carry over into adulthood. This finding is relevant to the study of the evolution of reproductive strategies, and of sex allocation in particular, because it shows that the costs-to-benefits balance of producing sons or daughters depends, besides other extrinsic factors, on the overall sex composition of the progeny.

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Chapter 5

Brownish, small and lousy barn swallows have greater natal dispersal propensity

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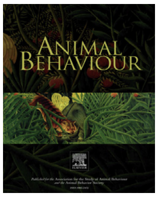

Brownish, small and lousy barn swallows have greater natal dispersal propensity

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Natal dispersal contributes to population dynamics and genetic structure. Individuals differ in whether or not they disperse and in the distance they travel from their natal site before settling to breed. Differences in natal dispersal are often associated with variation in other traits. These associations may arise because suites of morphological and behavioural traits are ultimately controlled by the same set of genes. The genes that control melanogenesis in vertebrates pleiotropically influence physiology and behaviour, including boldness and exploration. Because these personality traits predict dispersal, we tested the hypothesis that in the barn swallow, *Hirundo rustica*, melanic coloration predicts natal dispersal, using a solid matched case–control sampling design and a large sample. We found that males but not females with colour traits that reflect relatively more pheomelanic feather pigmentation were more likely to disperse, consistently with observations on the only other species for which dispersal in relation to plumage melanic coloration has so far been studied. To control for any confounding effects, we also analysed the association of dispersal with morphological traits and parasite infestation. Philopatric individuals were larger than dispersers, whereas dispersal strategy did not differ according to tail length, which is a sexually selected trait. Finally, philopatric females had a smaller infestation of a haematophagous louse fly. The present findings corroborate previous evidence that melanic coloration covaries with a suite of traits. In particular, they show that melanin-based plumage coloration predicts natal dispersal, independently of other factors also influencing dispersal. In addition, our results show that philopatric individuals were larger than dispersers possibly because individuals return to a benign natal place or because large body size confers an advantage in competitive interactions. Finally, they are compatible with the idea of host adaptation to local strains of a parasite with presumably small population size and low dispersing capacity.

Dispersing from the natal area to settle and breed in a different place is a prevailing life history strategy in vagile organisms, with major consequences for population dynamics and genetic structure (Clobert, Danchin, Dhondt, & Nichols, 2001; Greenwood, 1980; Greenwood & Harvey, 1982). Natal dispersal can serve diverse, nonalternative functions such as inbreeding avoidance or increasing the personal and indirect components of inclusive fitness by reducing competition among kin for limiting resources (Bowler & Benton, 2005; Dieckmann, O'Hara, & Weisser, 1999; Hamilton & May, 1977; Johnson & Gaines, 1990). However, dispersal entails costs in terms of time and energy, as well as increased risks and missed opportunities, as is the case when dispersers are more likely to incur predation or to lose the advantage of being adapted to local conditions (Bonte et al., 2012; but see Altwegg, Ringsby, & Sæther, 2000; Arcese, 1989). Variation in natal dispersal is often associated with differences in fitness traits (Clobert, Le Galliard, Cote, Meylan, & Massot, 2009), but disentangling the direction of any causal effect between dispersal and realized fitness has proven difficult.

Owing to its association with life history traits and the costs it entails, natal dispersal is believed to be directly targeted by intense natural selection. Empirical and theoretical studies suggest that variation in natal dispersal may be maintained by differences between individuals in the payoff of any specific dispersal strategy according to habitat quality and density of competitors, individual phenotype and sex (Altwegg et al., 2000; Barbraud, Johnson, & Bertault, 2003; Bowler & Benton, 2005; Greenwood, 1980; Massot, Clobert, Lorenzon, & Rossi, 2002; Nicolaus et al., 2012; Perrin & Mazalov, 1999). The extent of genetic variation in natal

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dispersal remains to be elucidated: environmental and early epigenetic effects appear to have been considered as predominating over genetic components (Clobert et al., 2001; Ims & Hjermann, 2001; Tschirren, Fitze, & Richner, 2007), but evidence is accumulating for heritability in dispersal distances (Clobert, 2000; Hansson, Bensch, & Hasselquist, 2003; Pasinelli, Schiegg, & Walters, 2004). In addition, variation in dispersal may be contributed by natural selection on linked traits that are relevant in other functional contexts (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). For example, it has been suggested that behavioural syndromes such as boldness and being explorative, which may be important in sociosexual or resource-finding contexts, are positively related to dispersal (Chapman et al., 2011; Fraser, Gilliam, Daley, Le, & Skalski, 2001; Jokela, Elovainio, Kivimaki, & Keltikangas-Jarvinen, 2008).

In turn, boldness and exploration behaviour have been found to be associated with melanin-based coloration (Mafli, Wakamatsu, & Roulin, 2011; Mateos-Gonzalez & Senar, 2012), thus adding to the large body of evidence for an association between melanin-based coloration and suites of functionally diverse behavioural and physiological traits (Ducrest, Keller, & Roulin, 2008; Roulin & Ducrest, 2011). The relationship between coloration and behaviour may have evolved to serve a signalling function (Andersson, 1994) or simply be a coincidental outcome of physiological constraints. Independently of any signalling function, however, the association of boldness/exploration with dispersal on the one hand and with coloration on the other leads us to expect an association between dispersal and coloration. Extensive within-population variation in melanin-based coloration that is commonly observed in birds and other vertebrates (Cramp, 1998; Hill & McGraw, 2006; Majerus, 1998) may thus partly reflect underlying variation in dispersal. Despite such premises, to the best of our knowledge the covariation between plumage coloration and dispersal has only been investigated in a single species, the barn owl, *Tyto alba*, in which individuals with darker, more pheomelanic plumage disperse over larger distances than less pheomelanic ones (van den Brink, Dreiss, & Roulin, 2012; Roulin, 2013).

In this study, we mainly focused on the covariation between observed natal dispersal decisions, that is, whether individuals were philopatric and were recruited as 1-year-old breeders in their natal colony or dispersed and settled as breeders in a different colony (hereafter ‘dispersal’), and melanin-based coloration of adult barn swallows, *Hirundo rustica*. Barn swallows show extensive variation in white-to-brownish ventral plumage coloration both in Palaearctic and in Nearctic populations (McGraw, Safran, & Wakamatsu, 2005; Safran, Neuman, McGraw, & Lovette, 2005; Saino, Romano, Rubolini, Teplitsky, et al., 2013; Vortman, Lotem, Dor, Lovette, & Safran, 2011). Darker individuals have larger concentrations of both pheomelanin and eumelanin in their belly feathers, and the darkness and saturation of belly colour increase with the concentration of pheomelanin relative to eumelanin (Saino, Romano, Rubolini, Teplitsky, et al., 2013). Hence, the coloration of the belly feathers reflects production of pheomelanin relative to eumelanin, which have partly common biosynthetic pathways (Hearing, 1998; Prota, 1992). In the present study we assumed that previous observations on pheo-/eumelanic determinism of coloration from the same population we studied here (Saino, Romano, Rubolini, Teplitsky, et al., 2013) hold also for the present sample of individuals. In addition, in this study we also assumed that observed dispersal at least partly reflects genetically based, underlying dispersal propensity. This assumption is warranted in particular in species such as the barn swallow for which weak or no constraints to natal dispersal (e.g. vagility, limitation of nesting places within dispersal range, social interactions including multipurpose territoriality) seem to operate (see Cramp, 1998; Møller, 1994; Turner, 2006).

Based on previous observations on the association between melanization and natal dispersal in the barn owl (van den Brink et al., 2012), we expected individuals that exhibit more pheomelanic relative to eumelanic coloration to show larger odds of dispersing. To test for a difference in coloration between individuals with different natal dispersal, while controlling for several potentially confounding effects, we adopted a solid sampling design in which we compared any 1-year-old philopatric individual with a dispersing individual of the same sex that immigrated in the same colony and year and was captured on the same date as the philopatric individual. In this way, we could control for both habitat quality at the settling site and temporal effects.

Any association between dispersal and melanin-based coloration, however, may be partly confounded by causal links between other traits and dispersal. Indeed, natal dispersal decisions are believed to depend on a constellation of extrinsic as well as phenotype-dependent factors which may also covary with melanization. In particular, we investigated the concomitant association of dispersal with morphological traits, including the expression of secondary sexual traits particularly in males (Balbontín et al., 2009; Belthoff & Dufty, 1998; Bonte & de la Peña, 2009; Clobert et al., 2009), as well as with the intensity of ectoparasite infestation (Gandon, 2002; Gandon, Capowiez, Dubois, Michalakis, & Olivieri, 1996).

The morphology of the locomotory apparatus may affect dispersal ability (Dawideit, Phillimore, Laube, Leisler, & Böhning-Gaese, 2009; de la Hera, Perez-Tris, & Telleria, 2012; Major, 2012; Roulin, 2006), although any such effect is more likely to occur in species in which dispersal distances are large relative to inherent vagility. In the barn swallow, however, migration distances are considerably larger, by three to four orders of magnitude, than dispersal distances (Turner, 2006). In fact, wing length or other nonsexually selected plumage traits were not found to predict dispersal (Scandolara et al., in press). Length of the outermost tail feathers of males is a sexually selected trait in our study population (Møller, 1994; Møller, Saino, Taramino, Galeotti, & Ferrario, 1998; Saino, Primmer, Ellegren, & Møller, 1997). According to the mate competition hypothesis (Dobson, 1982; Dobson & Jones, 1985), a positive relationship with philopatry might be expected, because long-tailed males should have an advantage in competition for a mate in our male-biased breeding population (Saino, Romano, Rubolini, Caprioli, et al., 2013). Rearing conditions may affect growth trajectories and thus final body size. We therefore expected offspring to use such beneficial effect of rearing conditions (‘silver spoon’ effect; Grafen, 1988) to assess habitat quality, being more philopatric when reared under benign conditions. We thus tested for a positive relationship between philopatry and skeletal body size.

Finally, parasites may play a major role in generating variation in dispersal strategies (Brown & Brown, 1992; Gandon, 2002; Gandon et al., 1996). This is the case because spatial structure of populations can influence the extent of reciprocal adaptation of the host and the parasite, affecting the relative costs of dispersing or being philopatric (see e.g. Gandon et al., 1996; Kaltz & Shykoff, 1998; Lively & Dybdhal, 2000; Tschirren et al., 2007). It is often assumed that, because of their shorter generation time and large genetically effective population size, parasites are advantaged over their coevolving hosts and are therefore more likely to be adapted to local host strains than vice versa (Gandon, 2002). Although empirical evidence suggests that this may be the most common scenario, results are mixed and no adaptation or even maladaptation to local hosts has been documented (e.g. Ebert, 1994; Dufva, 1996; Oppliger, Vernet, & Baez, 1999; Parker, 1985; and see Gandon, 2002). The outcome of host–parasite coevolutionary processes in terms of optimal host dispersal strategies is therefore likely to depend on the specific host–parasite system, on spatial and temporal variation in infection (Boulinier, McCoy, & Sorci, 2001), and on current infection of individual hosts. We thus analysed whether dispersal covaried with the intensity of infestation by the haematophagous louse fly, *Ornithomya biloba* (Diptera, Hippoboscidae), and chewing lice, which produce characteristic holes in the vanes of wing and tail feathers (Møller, 1994; Vas, Csörgö, Møller, & Rózsa, 2008). Little is known about the fundamental biology, including dispersal, of these parasites (see Methods) and on coevolution with their hosts. However, louse flies are likely to have both much smaller populations and opportunities for dispersal among host colonies compared with chewing lice (see Methods). Because in host–parasite systems the species with the higher migration (dispersal) rate is believed to evolve faster (Gandon, 2002), we expected that local adaptation, and thus a lower level of host infestation in philopatric hosts, was more likely to emerge from the analysis of louse fly than chewing lice abundance.

METHODS

Study Organism

Barn swallows are small (ca. 20 g), long-distance migratory, aerially insectivorous passerines that most often breed in colonies, seldom solitarily, inside rural buildings such as cowsheds, stables and garages (Ambrosini, Bani, Massimino, Fornasari, & Saino, 2011; Cramp, 1998; Møller, 1994, 2001; Turner, 2006). In northern Italy and southern Switzerland, adults arrive from their wintering range in sub-Saharan Africa in March–June and leave in August–October. The breeding season starts in April and may last until August when the last broods fledge. Socially monogamous pairs may have one to three clutches of two to seven eggs per breeding season. Eggs are incubated by the female for ca. 14 days (Turner, 2006). Hatching asynchrony is small, but non-negligible as it has consequences for nestling body mass rank throughout the nestling period and also in adulthood (Saino, Incagli, & Martinelli, 2001). Offspring fledge 18–20 days after hatching. Published estimates of natal dispersal distance (i.e. the distance between the natal colony and the colony of first reproduction, normally at age 1 year) are in the order of 5 km for males and 10 km for females (Turner, 2006). However, natal dispersal distances vary between geographical populations, probably according to availability of suitable breeding sites and also topography (Balbontín et al., 2009). Moreover, estimates of natal dispersal distance are likely to be heavily affected by sampling design. In the same study area in Switzerland in which part of this study was carried out, mean natal dispersal distance has been shown to be as small as 1.8 km for males and 3.3 km for females (Scandolara et al., in press). Overall, local recruitment is relatively rare, with 5% or fewer of the fledglings being recruited locally (Saino et al., 2012). The local recruitment datum, however, incorporates the effect of both mortality and dispersal. Dispersal is much more pronounced in females, as suggested by the five to eight times larger local recruitment rate of males, given an even sex ratio at fledging and similar mortality rates between the sexes. Breeding philopatry is high: fewer than 0.5% of adults breed on different farms in consecutive years, implying that no analysis of breeding dispersal in relation to coloration can be performed in our study population (Møller, 1994; Saino et al., 2012; see van den Brink et al., 2012).

In the same Swiss population in which the present study was partly carried out, natal dispersal of males was positively predicted by their position in the brood size hierarchy, while dispersal of both sexes was less likely to occur from large colonies located on farms with a large number of livestock (Scandolara et al., in press).

Overall, barn swallows have limited sexual dichromatism (Cramp, 1998). However, belly feathers of males tend to be darker than those of females (our unpublished data) and sex differences exist in the concentration of both eumelanin and pheomelanin in the belly feathers (Saino, Romano, Rubolini, Teplitsky, et al., 2013).

Study Areas and Field Procedures

We studied barn swallows in an area covering ca. 240 km^2 in northern Italy, east of Milan, during 1997–2010 and in an area in southern Switzerland, west of Bellinzona, in 2009–2012 (ca. 40 km^2). Barn swallow colonies were always located in rural buildings within farms scattered in intensively cultivated farmland. The distance between individual study farms and the nearest-neighbouring farm potentially hosting swallows was 0.3–1.0 km. The prevailing crops were maize, permanent pastures and hayfields in both study areas.

Every study year we did repeat capture sessions (April–June) of the adults (i.e. $\geq$1-year-old individuals) by placing mist nets before dawn at all the exits of the buildings in which barn swallows nest and normally spend the night during the breeding period. In this way we could capture the large majority of the members of individual colonies, as shown by observations with binoculars of individually marked (with colour rings and belly feather markings) birds and by the proportion of individuals that, at the last capture session of the season, were found not to have been previously captured during the same breeding season (see Saino et al., 2012). Because of high efficiency in capturing all the individuals in a colony and of high breeding philopatry, we could assume that all the adults that, in any given breeding season, were found not to have been captured in the previous breeding seasons were 1-year-old immigrants (i.e. individuals dispersing from their original colony and immigrating into our study colonies; hereafter ‘dispersers’). This is the case because those individuals that had not been captured previously were very unlikely to be locally breeding birds that had escaped capture in the previous breeding season and had dispersed, given the high breeding philopatry in our study populations (see above).

Local recruits (i.e. the philopatric individuals that were recruited as breeding adults in the colony in which they hatched) could be identified based on extensive ringing of nestlings on our study farms. Although it is possible that some local recruits went undetected because in some years we did not ring all the offspring on a farm, this is very unlikely to have confounded our analyses because local recruitment is very low (see above). In addition, in our analyses only one dispersing individual was matched to any given local recruit (see also below), so that the chances of including in the analyses a local recruit that was misclassified as an immigrant were reduced with respect to a design in which all the putative immigrants were included. Moreover, any inadvertent misclassification of a local recruit as an immigrant should have resulted in conservative results with respect to any phenotypic difference between immigrants and local recruits. We therefore regard this potential effect as negligible and, in any case, as a source of random noise rather than bias.

For the purposes of this study, among the morphological variables we measured upon first capture of adults, we considered the length of both of the outermost tail feathers (averaged for statistical analysis and expressed in mm), which is a sexually selected trait (Møller, 1994), the length of the innermost tail feather, the length of the right wing chord and keel length (expressed in mm × 100), which is as a proxy of body size. In Italy only, one feather was plucked from the white-brownish ventral plumage region for analysis of belly coloration by spectrophotometry (see below). Upon first capture, we also recorded the number of ectoparasitic louse flies that could be detected by carefully inspecting the plumage during ringing and measurement procedures (see also Saino, Calza, & Møller, 1998). As a proxy for the intensity of infestation by chewing lice we recorded the number of characteristic holes that amblyceran and ischnoceran lice make on tail (rectrices) and wing (remiges) feathers (see Vas et al., 2008).

Little is known about the dispersal ecology and biology of these ectoparasites. Louse flies may enter a pupal diapause after barn swallows leave the colonies in summer and adult parasites may emerge from puparia when swallows return from migration (Kennedy, Smith, & Smyth, 1975). Indeed, no louse flies were found on a sample of more than 100 swallows captured during spring migration in southern Italy (our personal observation) and more than 300 individuals captured in the Nigerian winter quarters of the same barn swallow population we studied here (Saino, Romano, Caprioli, et al., 2013), indicating that infestation occurs during spring. Mean intensity of infestation is in the order of a few parasites per adult host (range 0–5; present study). Including adult louse flies that are found in active nests, the average number of flies in a swallow colony per adult host is around three (S. Calza & N. Saino, unpublished data). Hence, counts of louse flies per host colony presumably range between a few and a few hundreds (see Ambrosini et al., 2012; Saino, Romano, Rubolini, Caprioli, et al., 2013 for colony sizes). Because louse flies are not found on barn swallows outside the breeding season, and breeding adults do not switch between different colonies during the same (or consecutive) breeding seasons, louse fly dispersal among swallow colonies may be rare and dependent on infested fledglings visiting other breeding colonies before leaving for autumn migration.

Chewing lice are probably much more numerous than louse flies and infest the host throughout the year, as indicated by observation of damage (holes) on newly grown feathers during moult in Africa, by direct observation of the parasites on the host's body, and by the increase in the extent of feather damage during the breeding season (Vas et al., 2008).

For each local recruit (i.e. a 1-year-old individual breeding in the same colony as it hatched) we a posteriori identified one dispersing individual (i.e. an individual that dispersed from its original colony and immigrated into one of our study colonies) for comparison. The disperser that was matched to any given recruit was a 1-year-old individual of the same sex that was captured on the same farm and on the same day as the focal local recruit. When more than one disperser fulfilled these criteria, the choice was randomized. Overall, the individuals included in the study were recruited in 25 colonies, each studied over 1–7 years. The number of recruits per farm ranged between 1 and 57.

The morphological and parasitological variables of both members of each local recruit–disperser pair of matched individuals were measured by the same observer (N.S. in Italy; C.S. in Switzerland). The morphological measurements we used in this study are known to have very high within-observer repeatability (e.g. Møller 1994; Saino, Romano, Rubolini, Teplitsky, et al., 2013).

Ethical Note

The study was carried out under ringing permit 0665 released by the Istituto Nazionale per la Fauna Selvatica, which issues all the relevant permissions required for this kind of work in Italy, and under the auspices of the 'Programma di cooperazione transfrontaliera Italia-Svizzera 2007–2013 – Indagine naturalistica e variabilità ambientale' (INTERREG project ID 15 7624065 – Misura 1.2). No approval from an ethics committee is currently required for this kind of study according to the existing legislation.

Spectrophotometric Colour Measurements

We measured reflectance of one plucked belly feather using an Avantes DH-2000 spectrometer, equipped with a combined deuterium–tungsten halogen light source, in a dark chamber (see Saino, Romano, Rubolini, Teplitsky, et al., 2013). Feather reflectance was always measured in duplicate and referred to white and black standards. The illuminated area was ca. 2.5 mm^2 and was centred 2.5 mm from the distal end of the feather, in a white to brownish region depending on the individual. Quantification of colour from the reflectance spectra was performed using the tetrachromatic colour space model by means of the TetraColorSpace program version 1a (Stoddard & Prum, 2008). This approach was preferred over alternative methods because it allows incorporation of information on both plumage reflectance and bird cone sensitivity to obtain biologically realistic colour metrics (see Antonov et al., 2010; Saino, Romano, Rubolini, Teplitsky, et al., 2013; Stoddard & Prum, 2008). In the analyses we assumed a UVS cone type retina and used spectral sensitivity of the blue tit, *Cyanistes caeruleus*, because the blue tit is the species most closely phylogenetically related to the barn swallow for which information on cone spectral sensitivity is implemented by TetraColorSpace. Idealized stimulation of the four cones of passerine birds were normalized to a sum of 1, so that tetrahedral coloration was described by a vector of {uv, s, m, l} values which represents stimulation of the cones sensitive to ultraviolet, short wavelengths, medium wavelengths and long wavelengths, respectively. Tetrahedral colour space vectors were then transformed into the spherical coordinates θ, φ and r (see Antonov et al., 2010; Stoddard & Prum, 2008). θ and φ roughly represent the red–green–blue (θ) and the ultraviolet (φ) components of hue, while r reflects colour saturation (or chroma). For barn swallow belly feathers, increasing θ values indicate paler, whitish coloration and a lower concentration of melanins, while decreasing θ indicates darker, brownish coloration and a higher concentration of melanins. Because the tetrahedral colour space is not a sphere, different hues vary in maximum potential chroma (r_{max}). In the analyses we therefore used 'achieved chroma', computed as $rA = r/r_{max}$.

Because the θ, φ and rA colour components are correlated, besides running the analyses on each colour component separately, we also ran a principal components analysis (PCA) to summarize the colour information, and used the individual scores on the first principal component that was extracted by the PCA.

Repeatability (Lessells & Boag, 1987) of the coloration variables estimated by measuring the same feather twice and measuring two feathers from the same individual exceeded 0.73 in all cases (Saino, Romano, Rubolini, Teplitsky, et al., 2013).

Statistical Analyses

The data set consisted of pairs of individuals: one local recruit and one disperser. Phenotypic variables were used as predictors of dispersal behaviour. Dispersal was coded as a dichotomous variable: local recruitment (code 0) and dispersal (code 1). The data were thus amenable to conditional logistic regression analysis (Breslow & Day, 1980; Hosmer & Lemeshow, 1989), where we modelled the odds of dispersal with pairs of matched individuals ('stratum') to account for the paired nature of the data. Conditional logistic regression models are equivalent to logistic regression models with a constant response, where the model contains no intercept and each predictor is expressed as the difference between the value of the case and the control for each case–control pair (Breslow & Day, 1980; Hosmer & Lemeshow, 1989). Positive values of the coefficients associated with the phenotypic predictors of dispersal indicate that the odds of leaving the original colony increased with the phenotypic values of the focal variable. Whenever possible, exact conditional inference was based on generating conditional distributions of the parameters of interest (see Allison, 2010). When this was not feasible because of computational constraints, we relied on maximum likelihood estimation. The fact that no exact test could be performed in these cases is unlikely to have altered the results, as the univariate analyses (see Table 1) gave consistent results with either estimation method, meaning that all the significant effects remained such whichever method we used (see Allison, 2010).

In exploratory analyses, we tested for a differential effect of morphological and parasitological variables (colour was measured only in Italy) on the odds of dispersal in either study area in conditional logistic regression models including the effect of the interaction between population and the focal variable of interest. In both sexes, the interaction effect was nonsignificant for all morphological and parasitological predictors of dispersal ($\chi^2_1 < 2.19$, $P > 0.138$), implying that any relationship between dispersal and phenotypic traits did not differ between the Italian and the Swiss study populations. We therefore pooled the data from the two populations in all subsequent analyses. Further details on model selection are reported in the Results section.

When univariate conditional logistic regressions on either sex disclosed significant effects on dispersal, we also subjected colour variables to PCA to try to reduce the dimensionality of the data. The decision on the number of principal components to be considered was based on the Kaiser–Guttman criterion (i.e. interpreting only the PCs with an eigenvalue larger than the mean eigenvalue for all PCs) and confirmed on the basis of the broken-stick criterion (see Borcard, Gillet, & Legendre, 2011).

Because multiple tests were run on the same sets of individuals, the risk of wrongly rejecting null hypotheses was inflated. ‘Traditional’ Bonferroni-like methods of correction for multiple tests may be too conservative, leading to considerable loss of statistical power. We thus relied on a less conservative false discovery rate (FDR) approach (see Pike, 2011) while adopting the two-stage sharpened algorithm for controlling FDRs (see Pike, 2011). Because the sets of individuals (males or females) for which information on morphology and parasitism was available were considerably larger than the sets for which information on colour was available, the FDR procedure was applied to either set of individuals of each sex separately. The significance threshold for FDR-corrected P values was set at 0.05.

All analyses were performed using SAS 9.2 (SAS Institute Inc., Cary, NC, U.S.A.) and SPSS13 (SPSS Inc., Upper Saddle River, NJ, U.S.A.).

RESULTS

We had information on the phenotype of 118–156 (depending on the trait) male and 20–28 female local recruits and their dispersing counterparts from the two study areas combined (see Table 1 for variable- and population-specific sample sizes).

Dispersal and Plumage Colour

Conditional logistic regression analyses of dispersal revealed partly different patterns of association with phenotypic traits in the two sexes. Melanin-based belly colour saturation significantly and positively predicted dispersal of males but not of females (Table 1, Fig. 1). In fact, for females the relationship was negative, although far from statistical significance. The relationship between dispersal and saturation did not differ significantly between the sexes (sex*saturation effect: $\chi^2_1 = 3.00$, $P = 0.083$). The lack of a sex*saturation effect on the odds of dispersal was due to the extremely large error associated with the coefficient for females (Table 1). However, the relationships between dispersal and colour saturation for the two sexes were opposite in sign and the strength of the association differed markedly between the sexes. There were no significant associations between dispersal of either sex and the θ or φ belly feather colour components (Table 1, Fig. 1). Because in males the three colour components were strongly correlated (correlation coefficient between θ and $\varphi = -0.64$; θ and $rA = -0.47$; φ and $rA = 0.208$; $N = 236$, $P < 0.002$ in all cases) we also ran a PCA on colour components (see Statistical Analyses). Based on the Kaiser–Guttman and ‘broken-stick’ criterion only the first principal component (PC1), which accounted for 64% of the variance in colour variables, was considered. PC1 was most strongly correlated with θ (loading = −0.91) and was also correlated with φ and rA (loadings = 0.80 and 0.66, respectively). Thus, increasing PC1 scores were associated with increasing pheomelanic darkness and saturation. Conditional regression analysis showed a significant effect of PC1 scores on the odds of dispersing (score statistic = 5.32, $P = 0.021$, coefficient = 0.349 ± 0.155). The positive sign of the coefficient implies that the odds of dispersing increased with relative pheomelanization and colour saturation.

Dispersal and Morphological Traits

The odds of being recruited into the natal colony rather than being a disperser were positively predicted by body size in both sexes (Table 1, Fig. 2). A conditional logistic regression model including the interaction between keel length and sex showed that the slope of the association of dispersal with body size differed significantly between the two sexes ($\chi^2_1 = 4.40$, $P = 0.036$): the change in the odds of dispersal per unit change in body mass was larger among females than among males. No significant association between dispersal and tail length was observed in either sex (Table 1).

Dispersal and Ectoparasite Load

The odds of dispersal of males were negatively predicted by the intensity of infestation by chewing lice, implying that local recruits harboured more chewing lice than dispersing individuals, whereas dispersal of males was not predicted by infestation by louse flies (Table 1, Fig. 3). Conversely, dispersal of females was positively predicted by louse fly infestation (i.e. local recruits harboured fewer flies) but was not predicted by chewing lice infestation (Table 1, Fig. 3). Conditional exact tests provided statistically significant

Table 1
Univariate conditional logistic regression models of dispersal in relation to phenotype and parasitism

	Males				Females			
Predictor	N (IT, CH)	Score	Exact P	Coefficient (SE)	N (IT, CH)	Score	Exact P	Coefficient (SE)
θ colour component	236	1.79	0.182	−3.84 (2.897)	40	1.18	0.286	5.559 (5.235)
φ colour component	236	2.52	0.113	2.645 (1.693)	40	0.00	0.999	0.003 (3.266)
Colour saturation (rA)	236	8.16	**0.004**	6.315 (2.279)	40	0.86	0.371	−6.199 (6.856)
Tail length	312 (236, 76)	2.82	0.094	0.032 (0.019)	56 (40, 16)	0.730	0.409	−0.047 (0.055)
Keel length	300 (236, 64)	8.64	**0.003**	−0.005 (0.002)	52 (38, 14)	12.43	**<0.001**	−0.036 (0.015)
Chewing lice infestation	300 (236, 64)	6.94	**0.008**	−0.020 (0.008)	54 (40, 14)	0.10	0.773	−0.004 (0.014)
Louse fly infestation	300 (236, 64)	0.33	0.620	−0.082 (0.144)	54 (40, 14)	4.47	**0.019**	1.428 (0.719)

The odds of dispersing (versus being recruited in the colony of origin) are modelled. The column ‘N (IT, CH)’ shows the total sample size and the sample size for the Italian (IT) and the Swiss (CH) populations. Colour was measured only in Italy. Probability values from exact score tests are presented. Bold values were significant also after controlling for the increase in the risk of wrongly rejecting a null hypothesis by the false discovery rates procedure.

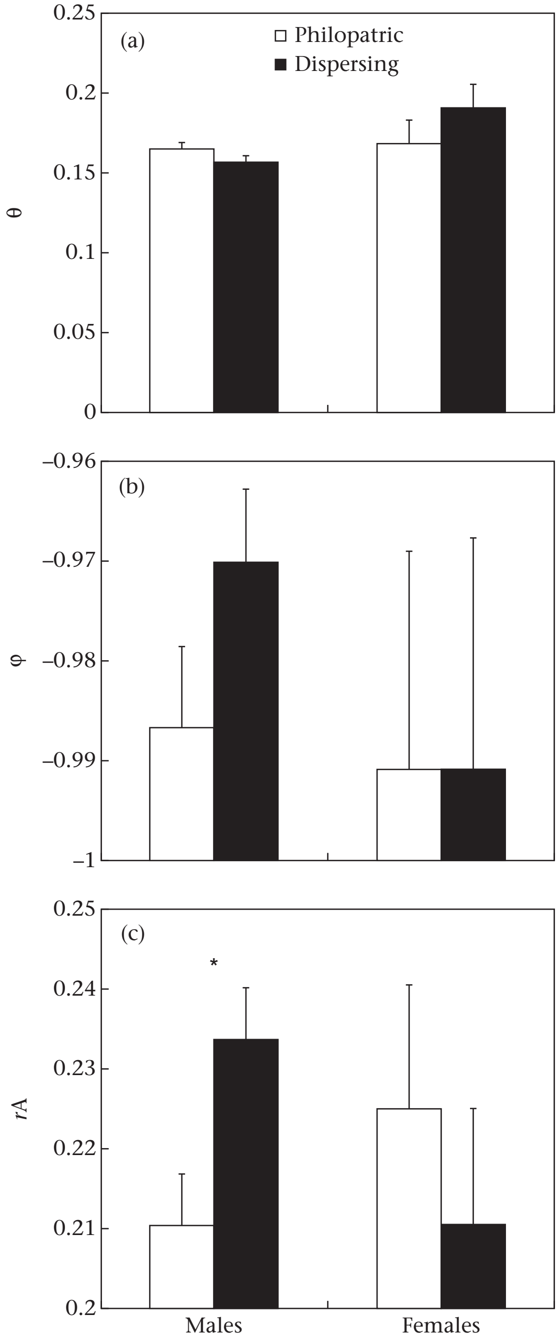

Figure 1. Mean + SE tetrahedral colour component values of philopatric and dispersing male and female barn swallows. (a) The red–green–blue (θ) and (b) the ultraviolet (φ) components of hue, and (c) colour saturation (*r*A; see also Spectrophotometric Colour Measurements in the Methods). Small θ and large φ or *r*A values indicate increasing pheomelanin relative to eumelanin concentrations. Sample sizes are reported in Table 1. An asterisk indicates that the odds of dispersing were significantly associated with the focal variable.

evidence for a differential effect of louse fly (score statistic = 5.68, $P = 0.017$) but not of chewing lice infestation on dispersal of the two sexes (score statistic = 1.07, $P = 0.308$).

Dispersal in Relation to Multiple Phenotypic Traits

The main aim of this study was to test for a covariation of dispersal and colour while controlling for potentially confounding phenotypic and parasitological variables. Some phenotypic variables were reciprocally correlated (e.g. colour variables) and we had no a priori expectations on interaction effects among the phenotypic variables on dispersal. To avoid multicollinearity and model overparametrization problems particularly for females, which had the smaller sample size, we refrained from applying complex multivariate models that included all phenotypic variables with their interactions as predictors of dispersal. We instead applied conditional logistic regressions that included only the variables that significantly predicted dispersal in univariate models on either sex (see Table 1).

There were no significant two-way interaction effects between colour saturation, body size and chewing lice infestation on dispersal of males ($\chi^2_1 < 0.70$, $P > 0.40$). A simplified model excluding any interaction effect confirmed the positive effect of colour saturation ($\chi^2_1 = 10.04$, $P = 0.002$) and the negative effect of keel length ($\chi^2_1 = 9.40$, $P = 0.002$) and chewing lice infestation ($\chi^2_1 = 9.11$, $P = 0.003$) on dispersal of males.

Among females, dispersal was not predicted by the interaction between keel length and louse fly infestation ($\chi^2_1 = 0.11$, $P > 0.741$). A simplified model including only the main effects confirmed that the odds of dispersing declined significantly with body size ($\chi^2_1 = 4.64$, $P = 0.031$), while a marginally nonsignificant positive association between dispersal and louse fly infestation existed ($\chi^2_1 = 3.34$, $P = 0.067$), suggesting consistency with the results of univariate analyses.

DISCUSSION

We analysed natal dispersal in barn swallows and found that philopatric individuals differed from dispersers in a number of phenotypic traits, including melanic plumage coloration, body size and parasite load. The associations between these traits and dispersal were independent of the concomitant association with other traits, but were dependent on sex. In the analyses, by matching philopatric and dispersing individuals for sex, year, date and colony we effectively controlled for a number of potentially confounding temporal and local effects.

Dispersal and Plumage Colour

The association between colour and natal dispersal was the main focus of our study because a theoretical background exists to interpret any covariation between melanic coloration and dispersal (Ducrest et al., 2008; Roulin & Ducrest, 2011), but little empirical information on this association exists. Indeed, we are aware of only one species for which natal dispersal has been analysed in relation to plumage melanization: in the barn owl, darker reddish, more pheomelanic individuals moved further from their natal site than paler, less pheomelanic ones (van den Brink et al., 2012; Roulin, 2013). In male barn swallows, the pattern of natal dispersal was consistent with that observed in the barn owl, as individuals with darker, more saturated colour were more likely to disperse. Darker reddish, more saturated belly feather colour is associated with increasing ratios of pheomelanin to eumelanin (Saino, Romano, Rubolini, Teplitsky, et al., 2013). This implies that individuals with more pheomelanic relative to eumelanic coloration were more likely to disperse. Our findings suggest that variation in dispersal is consistently associated with melanism in phylogenetically distant species with broadly different life histories. In the barn owl, pheomelanization rather than eumelanization predicted dispersal, suggesting that the association between dispersal and coloration in the barn swallow might be ultimately driven by pheomelanization per se, rather than by relative investment in pheomelanization compared to eumelanization.

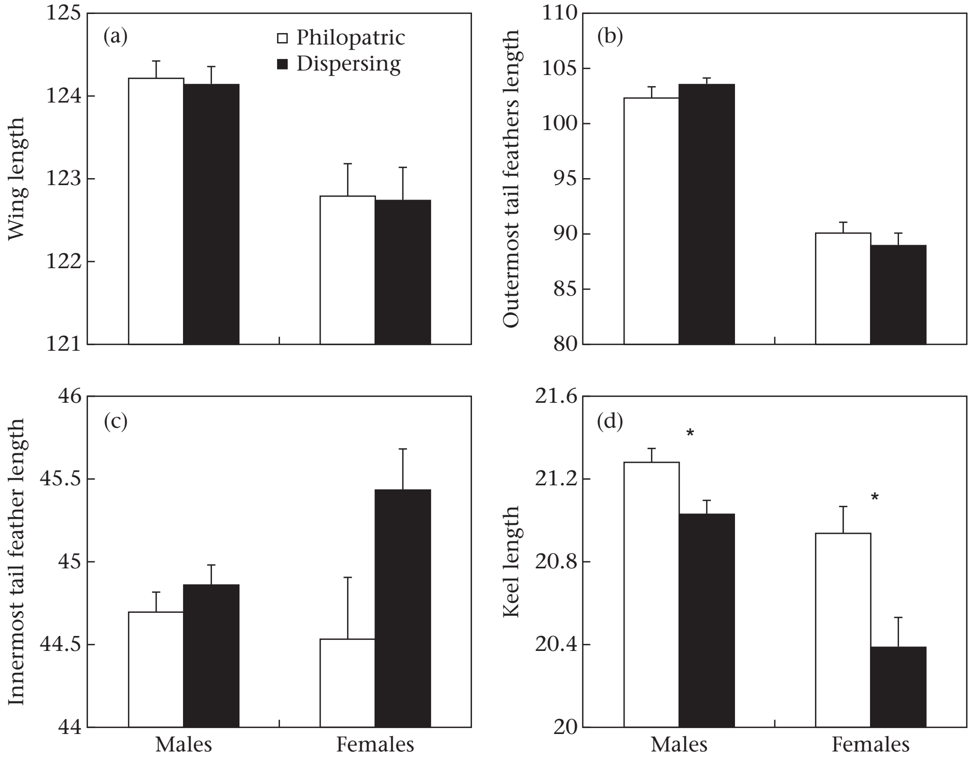

Figure 2. Mean + SE morphological trait values (in mm) of philopatric and dispersing male and female barn swallows. (a) Wing length, (b) outermost tail feather length, (c) innermost tail feather length and (d) keel length. Sample sizes are reported in Table 1. An asterisk indicates that the odds of dispersing were significantly associated with the focal variable.

In the present study, the slopes of the relationships between dispersal and coloration did not differ between the sexes, although they were opposite in sign. This was mainly due to the large error associated with the parameter estimate for females. However, the relationship was considerably stronger, being highly significant, in males than in females, for which it was far from statistical significance. This difference may suggest a role of sexual selection in the evolution of this relationship. In the present sample of males, infestation by chewing lice was larger among relatively less pheomelanic individuals (Spearman's ρ with $\theta = 0.131$ and with $\varphi = -0.167$, $P < 0.05$ and $N = 236$ in both cases). In addition, darker, presumably relatively more pheomelanic individuals have been shown to have greater success in sperm competition in other barn swallow populations (Vortman et al., 2011), although information on sexual selection from our study population is not yet available. These pieces of evidence combined may suggest that dispersal and coloration are linked traits under sexual selection, with dispersing individuals harbouring fewer parasites and having greater success in sperm competition.

At a proximate level, the association between dispersal and melanization in barn swallow males may be mediated by exploration. Dispersal covaries with boldness and exploration (Budaev, 1997; Dingemanse, Both, Van Noordwijk, Rutten, & Drent, 2003; see van den Brink et al., 2012). Darker, more melanic siskin, *Carduelis spinus*, males have been found to be more active at exploration (Mateos-Gonzalez & Senar, 2012). Hence, dispersal of more pheomelanic male barn swallows may be mediated by their exploration tendencies.

Dispersal behaviour is generally considered to be under strong selection (Clobert et al., 2001). Dispersing individuals may face diverse costs at all stages of the dispersal process (Bonte et al., 2012). On the other hand, philopatry may also entail costs in terms of both local competition with kin for limiting resources and inbreeding (Bowler & Benton, 2005; Hamilton & May, 1977; Johnson & Gaines, 1990). The mechanisms that maintain variation in dispersal in relation to melanization of male barn swallows are open to speculation. It has been hypothesized that because of antagonistically pleiotropic effects that some of the genes that control melanization have on major life history traits (Ducrest et al., 2008), between-individual variation in melanin-based coloration may reflect underlying variation in life history strategies that are associated with a minor or no net difference in fitness. Philopatric males have been shown to be more viable at least among barn swallows breeding in Spain (Balbontín et al., 2009; but see Saino et al., 2012 for different results based on a small sample). In addition, in our study population, darker, relatively more pheomelanic males (but not females) are less viable (Saino, Romano, Rubolini, Ambrosini, et al., 2013). The present findings are thus consistent with the expectation from previous studies of barn swallows because they show that philopatric individuals have relatively less pheomelanic coloration. Overall, available data from barn swallows thus suggest that philopatric, paler and relatively less pheomelanic males may accrue a viability advantage over dispersing, darker and more pheomelanic males, which may in turn be more successful in sperm competition. This is consistent with the general idea that the evolution of behavioural syndromes can maintain polymorphism in coping strategies (Wolf, Sander van Doorn, Leimar, & Weissing, 2007) and, specifically, that colour variation is associated with variation in life history strategies with similar fitness payoffs.

Several additional functional interpretations can be devised for the difference we observed in dispersal in relation to melanization (see van den Brink et al., 2012). Colour-related susceptibility to the consequences of inbreeding, which has been hypothesized for barn owls, may not be important in causing differential dispersal because close inbreeding is likely to be rare in barn swallows, given large population sizes within the normal natal dispersal range,

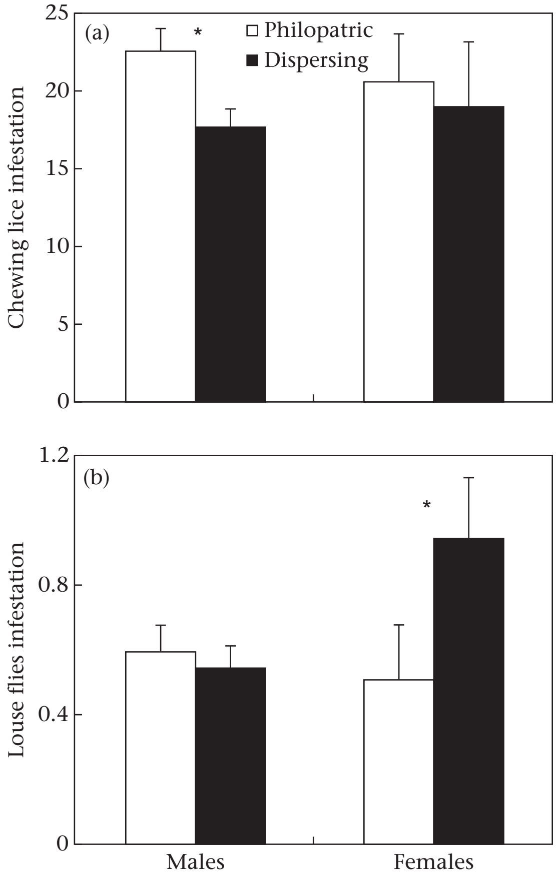

Figure 3. Mean + SE parasite infestation (counts; see Study Areas and Field Procedures in the Methods) of philopatric and dispersing male and female barn swallows. (a) Chewing lice and (b) louse flies. Sample sizes are reported in Table 1. An asterisk indicates that the odds of dispersing were significantly associated with the focal variable.

partial temporal segregation among generations and partial spatial segregation between opposite-sex siblings owing to females being less philopatric and dispersing further. Adaptation of colour variants to local conditions at the colony/natal area level could also be invoked (Dreiss et al., 2012). This idea has not yet been tested formally. However, our study colonies were scattered over a large area and much of the variation in ecological conditions, in terms of nesting or foraging habitat, occurs over much shorter distances than those encompassed by the study area itself (our unpublished data). Hence, the possibility that our study farms were systematically located in habitats that favoured immigration of more pheomelanic individuals seems remote. It has also been suggested that melanization could be at linkage disequilibrium with traits that are functionally related to dispersal by, for example, affecting locomotion. Dispersal distances of barn swallows are three to four orders of magnitude smaller than migration distances and it therefore seems unlikely that ability to disperse is restricted by morphology of, for example, the flight apparatus (see also above).

Dispersal and Morphological Traits

Tail length, which is a sexually selected trait in males from our study population (Saino et al., 1997), did not predict dispersal significantly, lending no support to the competition for mates hypothesis, which posits that less attractive males should disperse to avoid competition for mates (Balbontín et al., 2009; Dobson, 1982; Dobson & Jones, 1985). Yet, there was a strong, negative effect of body size on dispersal in both sexes, this effect being significantly larger among females. Dispersal declines with hatching date and significantly so only in females (Scandolara et al., in press). However, in the present sample of philopatric individuals for which hatching date was known, there was no association with keel length (ANOVA controlling for population: effect of hatching date: $F_{1,147} = 1.21$, $P = 0.273$), implying that the association between philopatry and body size was not the spurious result of dispersal depending on seasonal effects that concomitantly affected body size. Yet, large body size may result from favourable rearing conditions, and large offspring may cue onto such conditions or onto their own phenotype to decide not to disperse from a favourable habitat. This effect could be more pronounced among females, which may be more sensitive to habitat quality given their larger reproductive investment.

Dispersal and Ectoparasitism

We also identified differential variation in dispersal according to host sex and parasite species. Males that were more heavily infested by feather lice were less likely to disperse, whereas larger counts of louse flies were recorded among dispersing than philopatric females. Louse flies probably infest their host upon arrival to the breeding colony. Because of extremely high breeding philopatry of the host and of the life cycle of louse flies (see Study Areas and Field Procedures), dispersal of louse flies and thus gene flow among host colonies can be expected to be small. Greater infestation among immigrants may therefore suggest that female hosts are more resistant to parasite strains from their original colony. This is in agreement with our expectation that any local host adaptation was more likely to emerge for louse flies than for chewing lice (Gandon, 2002). Virulence of louse flies to nestlings (Saino et al., 1998) and potentially also to adults may thus be a cost of natal dispersal for female barn swallows.

The dynamics of transmission of feather lice are unknown. Adult hosts harbour the parasite all year round (our personal observation; see also Study Areas and Field Procedures). Because feather holes are normally found also on yearlings during moult in Africa, dispersal and gene flow of this parasite among host colonies must be large, thanks to large host natal dispersal. Hence, the present findings suggest that either philopatric hosts are inherently more susceptible to parasite infestation in the year of hatching (or to reinfestation upon return to the natal colony) or intensity of infestation is itself a determinant of dispersal. The latter could be the case if the parasite has debilitating/aerodynamic effects that hinder prospecting for breeding sites either before or after the first migration to Africa. Alternatively, chewing lice infestation may covary with philopatry as a spurious effect of the association between melanization and both dispersal and parasitism (see above).

In conclusion, we have observed that natal dispersal of barn swallows is related to melanization, as males that allocated relatively more to pheomelanization than eumelanization had greater odds of dispersing. This is consistent with the pattern observed in the only other avian model for which natal dispersal has been analysed in relation to melanization. The association between natal dispersal and melanization corroborates previous evidence from the same or other barn swallow populations for an association of melanization with major life history traits. Extensive variation in plumage melanization within bird populations thus calls for more studies on the covariation with dispersal behaviour. The association between dispersal and colour was independent of any effect of body size, which was found to be larger in philopatric individuals of both sexes, possibly because of fidelity to a natal place with favourable rearing conditions. Finally, the intensity of infestation by ectoparasites was found to predict natal dispersal. Lower infestation by louse flies in philopatric females, in particular, suggests adaptation to local strains of a parasite with probably little gene flow among hosts' colonies.

Acknowledgments

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DISCUSSION AND CONCLUSIONS

Concluding remarks

The present thesis investigates different aspects of the two main movements of birds - migration and natal dispersal - using the barn swallow as an ideal model species.

First, the dissertation provides novel findings about the migration of this long-distance migratory bird, one of the phenomena that have fascinated people since ancient times. I successfully used a new technology, based on light-level 'geolocators', by which I could gather more information on the migration of barn swallows than it could be collected over more than one century of intense ringing activity of this species. Moreover, the present work also gives an important contribution to the evaluation of possible drawbacks of this technology, for passerines in general, and for aerially insectivorours species, which may be particularly susceptible to geolocator deployment, in particular.

Second, I studied natal dispersal in barn swallows, giving a fundamental contribution to the knowledge of this ecological process from different points of view, and identifying several factors that affect dispersal decisions and that act at different scale and stage of the individual life history.

Both the results on migration and on natal dispersal may have also a great importance in order to plan appropriate conservation measures at the breeding sites and on the wintering grounds. Indeed, several barn swallow geographical populations, including the ones I studied, are declining, probably as a result of diverse factors that act both in breeding and in the wintering areas. The detailed knowledge of the geographical positions and movements in the non-breeding areas and along the migration routes is the first and indispensable step to program interventions of conservation in the wintering areas. In the breeding sites, for instance, I have demonstrated that the presence of livestock is a key factor for the local recruitment of young; so its maintenance in the farms may contribute to buffering the population decline of this species. Hence, my findings on the two topics can have in the future also a practical application for the conservation of the breeding populations of this declining, flagship bird species.

Migration

The aim of this part (**Chapters 1-2**) was to fill the gap in our current knowledge of the migration of small-size migratory birds, so far hampered by technological limitations. The barn swallow was an ideal model species because it feeds on aerial insects and spends a large proportion of its diurnal life on the wing, so the application of a external device that influences the drag is easier to detect. Furthermore, adults are extremely philopatric, and this feature allowed us to recover a relatively large proportion of the light-level geolocators.

In **Chapter 1**, I investigated migration and wintering of three geographical populations (one in Switzerland and two in northern Italy) of barn swallows with this advanced device. The barn swallow is one of the smallest species on which geolocators have been successfully deployed to date. The data set consisting of 103 annual tracks is the largest dataset available for any migratory passerine.

Thanks to this research, I identified in Central Africa, in a region 1000 km in radius centred in Cameroon, the main wintering area of the three geographical populations. Only 5 males reached southern Africa, covering more than 10,000 km between breeding and wintering sites. Most individuals occupied only a single site during their stay south of the Sahara. The dataset allowed, for the first time for a small bird, to compare migration behaviour of males and females based on a solid sample size, and to compare different geographical populations over two-years of investigation.

This huge dataset will now provide the basis to investigate in the near future many other still open and vividly debated questions in bird migration studies. For instance, it will be possible to analyse aspects such as the level of migratory connectivity at small geographical scale, the evolution of protandry, the differences between migration of adults and first-year birds and, thanks to individuals following in subsequent years, the fidelity to the wintering grounds and migrations routes. Moreover, using weather data (ERA-Interim) and remote sensing (NDVI), migration and wintering decisions will be analysed to evaluate how variation in local weather conditions (wind, temperature, rainfall) influence migratory flights and the decisions to leave or stop-over.

In short, this research confirmed that miniaturized light-level geolocators are extremely useful and are revolutionizing the study of small-size migratory birds, making it possible to follow the annual cycle of large samples of individuals and obtaining information that were unthinkable just a few years ago.

In **Chapter 2**, I made an important contribution in testing this technique for the study of bird migrations. I investigated the possible long-term effect of two miniaturized geolocator models and the impact of this new technology on return rate, morphological traits and breeding success of adult swallows.

Using an experimental approach, with geolocator and control individuals from the three geographical populations, I showed that geolocators had a negative impact on survival and reproduction. The first important and negative long-term effect was that the geolocators reduced annual survival probabilities depending on year, sex, and how birds that lost the device were considered, with more markedly negative effects on females equipped with the heavier geolocator model with longer light stalk that was deployed in 2010. Another negative effect was found among birds equipped with the 2010 model: the onset of reproduction in the subsequent year was delayed and females laid smaller first clutches compared to controls.

Based on the results on the effects of the first geolocator model, a new model was developed in 2011, which had smaller weight and shorter light stalk, thus reducing drag. This new device slightly enhanced the survival of females but not that of males, and mitigated the negative carry-over effects on subsequent reproduction.

Equipping parents with geolocators while they were attending their brood did not affect nestling body mass or fledging success, so I didn't found short-term effects of the application of this device.

To conclude, my findings on this subject suggested that, before extensively applying the devices, pilot experiments are mandatory to test for return rate and fitness effects involving treated and control subjects.

Taken together, the results of **Chapter 1 and Chapter 2** show that the geolocators are revolutionizing the world of research in avian migration. One assumption commonly accepted of this kind of study is that deployment of these devices does not markedly affect migration behaviour. It is therefore important to continue improving the performance of these year-round tagging devices, to further minimize negative impacts.

Natal dispersal

The aim of the second part (**Chapters 3-5**) of this thesis was to explore different aspects of natal dispersal. The barn swallow was a good model species also to study this topic because the nestlings can be ringed and recovered year after year and, even if the recovery rate is very low, with a great effort it was possible to obtain a large dataset to analyse.

In **Chapter 3**, I identified diverse factors that affect the natal dispersal decisions of barn swallows. I found that sex strongly affected both dispersal propensity and distance, with females being the most dispersing sex, as expected for birds in general. Besides, natal dispersal of males was positively predicted by their position in the brood size hierarchy, while dispersal of both sexes was less likely to occur from large colonies located on farms with a large number of livestock, that is demonstrated to be an important factor for swallows in breeding site choice.

I have then demonstrated that the decision about dispersing or not and the decision about the dispersal distance are two separate processes, which are at least partly controlled by different factors.

Using the data obtained from natal dispersal, in **Chapter 4** I made another step and focused on long-term consequences of family sex composition on offspring of either sex; before this research only one study existed on this topic in birds. I have analysed the carry over effect of brood sex composition on adult phenotype and breeding performance.

The results showed that both sexes had different effects on opposite-sex siblings. Male offspring with more sisters had shorter wing length, an aerodynamically important trait, and tail length, a condition dependent, sexually selected trait. On the other hand, female offspring with an increasing proportion of male siblings and also with increasing brood size showed a decline in breeding success; their tail length decreased with increasing brood size, but more steeply so when they grew with more female siblings. Finally, body size also declined with increasing brood size. In conclusion, I have found evidence for reciprocal negative effects between offspring of either sex, and this demonstrates that social environment had major consequences for phenotype and breeding performance in adulthood. This finding give a contribution to the understanding of the evolution of reproductive strategies, showing that optimal parental sex allocation decisions depend not simply on additive fitness costs and benefits of producing males or females, but also on the long-term effects that sons and daughters exert on each other.

In **Chapter 5**, I found that males, and not females swallows, with colour traits that reflect relatively more pheomelanic feather pigmentation were more likely to disperse, confirming previous results on barn owl, the only other species for which dispersal in relation to plumage melanic coloration has so far been studied.

I have also analysed the association of dispersal with morphological traits, and found that philopatric individuals were more numerous than dispersers, possibly because individuals return to a favourable natal place, or because large body size confers an advantage in competitive interactions, whereas dispersal strategy did not differ according to tail length, which is a sexually selected trait. Finally, the intensity of infestation by ectoparasites was found to predict natal dispersal. Philopatric females had smaller infestation by an haematophagous louse fly, and this is compatible with the idea of host adaptation to local strains of a parasite with presumably small population size and low dispersing capacity with probably little gene flow among hosts' colonies.

Appendix 1

Complete phenological data for individual loggers, and SRP latitude and longitude.

Age is coded as adult (1) or juvenile (0) bird when the logger was deployed.

ID	**Age**	**Sex**	**Area**	**Departure from the breeding colony**	**Arrival to the sub-Saharan residence area**	**Departure to the sub-Saharan residence area**	**Arrival to the breeding colony**	**SRP latitude**	**SRP longitude**
1RH	1	1	piem	246	280			8.63	14.13
1RZ	1	1	magad	257	284	76	99	5.88	15.07
1SN	1	1	magad	257	269	79	101	3.25	18.34
1ST	1	2	magad	255	292	65	111	11.11	2.06
1SU	1	1	magad	255	279			-0.64	14.51
1TA	1	1	piem	253	277	79	101	5.79	11.62
1TD	1	2	piem	262	297	105	119	9.31	12.54
1TE	1	1	piem	254	281	62	89	9.94	8.53
1TF	1	1	piem	253	279	63	88	5.04	9.44
1TG	1	1	magad	245					
1TH	1	2	piem	235	280	61	83	9.57	15.50
1TJ	1	1	magad	252					
1TQ	1	1	magad	257	269	55	76	13.61	10.41
1TS	1	1	piem	255	279	84	92	14.60	-4.47
1TV	1	1	piem	255	292	59	106	1.61	13.60
1UE	1	1	magad	252	285	66		11.30	7.48
1UH	1	2	magad	253	272	80	110	10.22	6.76
1UJ	1	1	magad	257	278	64	83	11.83	17.34
1UP	1	1	piem	255	303			7.61	16.81
1UR	1	1	magad	258					
1US	1	1	piem	255					
1UY	1	2	magad	232	289	73	93	11.19	17.30
1VP	1	2	magad	254	284	92	127	-0.28	13.57
1WG	1	2	magad	252	276	55		8.50	10.54
1WH	1	1	magad	253	287			2.91	12.94
1WW	1	2	magad	251	277	73	101	2.98	8.74
1XI	1	2	magad	252					
1XJ	1	2	piem	257	273	66	97	7.71	9.45
1XQ	1	1	piem	256	299	62	108	8.25	14.32
1XR	1	1	magad	252	284	68	102	7.37	15.28
1XT	1	1	magad	252	284	77	101	4.87	11.58
1YA	1	1	magad	252	284			-0.60	9.53
1YD	1	1	magad	252	286	66	122	-26.59	29.45

1YW	1	1	magad	253	288	76	99	9.21	7.45
1ZP	1	1	magad	242	282	70		2.84	10.30
1ZS	1	2	magad	242	273			2.18	9.56
1ZV	1	1	magad	254	269			5.16	15.72
1ZW	1	2	magad	252	271			7.55	6.45
1ZY	1	2	magad	252	276	75	101	5.85	18.71
2AA	1	1	magad	251	286	76	102	12.57	10.12
2AC	1	2	magad	252					
2AI	1	2	magad	252	275			15.67	-9.94
2AL	1	1	magad	252	274	61		9.43	13.62
2AR	1	2	magad	256	280			7.26	8.95
2AT	1	1	piem	252	268			4.35	12.97
2AZ	1	2	piem	242	277			10.62	16.44
2BE	1	1	magad	252	274	79	106	6.96	12.52
2BJ	1	1	piem	255	285	79	122	8.74	4.19
2BO	1	2	piem	235	284			9.42	8.63
2BT	1	1	piem	254					
2BV	1	1	piem	255	284	72	101	4.17	14.94
2CA	1	2	magad	252	286	99	130	6.43	11.16
2CH	1	2	piem	253	277			5.99	10.27
2CJ	1	1	piem	265	275	76	102	2.31	11.27
2CT	1	1	magad	261	277	76	114	6.97	11.12
2DA	1	1	magad	256	306	90	110	10.07	15.24
2DB	1	1	piem	252	290	76	110	9.99	12.04
2DC	1	2	magad	262	296			-0.70	13.86
2DF	1	1	piem	252	281	75	97	8.61	18.45
2DH	1	2	piem	257	273	75	101	4.21	17.07
2DS	1	2	piem	251					
2EF	1	1	piem	253	279			20.40	-4.05
2EU	1	1	piem	251	284			2.98	13.41
2EW	1	1	piem	248	268			3.50	17.50
2EX	1	1	lomb	254	270	71	97	2.15	11.14
2FR	1	2	lomb	255	279	75	100	5.31	17.35
2FT	1	1	piem	253	277			9.49	11.39
2GK	1	1	lomb	249	268	61	74	3.17	18.53
3CX	0	1	magad	249	293	124	147		
3MP	0	1	magad	251	305	72	125		
3MY	1	1	magad	250	289	70	124	3.26	17.84
3NH	1	2	magad	232	287	96	114	6.04	8.72
3QM	1	2	magad	251	288	113	130	0.21	13.61
3QX	1	1	magad	252	286	58	95	6.79	19.38
3RD	1	1	magad	237	283	52	116	-27.84	24.02
3RK	1	1	magad	234	287	84	113	6.42	10.70
3RM	1	1	magad	253	291	87	108	5.64	15.64
3RN	1	1	magad	250	290	79	125	-23.75	23.54

3RR	1	1	magad	249	291	93		3.00	13.43
3SI	1	1	piem	255	289	68	123	-0.23	13.13
3SP	1	1	piem	254	289	106	117	5.87	18.96
3SS	1	1	piem	249	278	74	116	6.36	9.32
3ST	1	2	magad	251	280	68	128	9.63	2.91
3TR	1	1	piem			55	103	7.11	21.30
5AE	1	2	magad	248	277	75	103	3.07	15.90
5AU	1	1	magad	249	294	94	117	-0.24	15.80
5AY	1	1	lomb			93	113	6.02	6.31
5BM	1	1	lomb	241	271	76	101	0.80	10.45
5BN	1	1	lomb	249	269	94	110	-0.06	12.67
5BO	1	2	lomb	250	300	63	101	6.06	16.92
5BS	1	1	lomb	245	279	67	97	1.47	17.16
5CX	1	1	lomb	248					
5FB	1	2	piem	254	285	74	100	5.61	11.34
5FC	1	1	piem	249	294	58	101	-19.55	17.41
5FH	1	2	lomb	250	271	72	114	3.28	10.69
5FY	1	2	piem	233	284	83	106	5.40	15.30
5GD	1	1	piem	251	273	60	93	1.87	15.82
5GM	1	2	lomb	244	275	47	96	-0.48	25.01
5GN	1	1	piem	251	273	60	71	8.09	15.73
5HC	1	1	lomb	248	276	67	106	-0.41	15.30
5HE	1	1	lomb	249	287	98	114	6.31	11.36
5HR	1	1	lomb	236	272			6.89	13.64
5ID	1	1	lomb	250	309	68	108	-32.37	21.06
5II	0	2	magad	251	296	122	140		
5IK	0	2	magad	248	277	120	152		
5IO	1	1	lomb	251	283			1.47	14.31
5JK	1	1	lomb	258	281	67	103	5.03	13.77
5LK	0	1	magad	251	298	104	119		

Appendix 2

List of individual stationary periods in sub-Saharan residence areas.

These data were used to produce the maps of wintering locations. The longitude and latitude of the longest stationary period were taken as the SPR latitude and longitude for each individual. Dates are expressed as days since Jan 1 of the initial migration cycle for each logger ID.

ID	Longitude	Latitude	Month	Start date stationary period	Final date stationary period
1RH	14.13	8.63	11	288	341
1RZ	15.07	5.88	10	289	422
1SN	11.56	8.03	10	288	311
1SN	18.34	3.25	2	324	422
1ST	2.06	11.11	10	292	422
1SU	14.51	-0.64	11	288	355
1TA	11.62	5.79	10	288	422
1TD	13.66	7.48	11	297	381
1TD	12.54	9.31	2	385	470
1TE	8.53	9.94	10	288	422
1TF	11.15	3.69	11	288	345
1TF	9.44	5.04	2	362	422
1TH	13.68	12.38	2	393	422
1TH	15.50	9.57	11	288	392
1TQ	10.41	13.61	10	288	420
1TS	-3.10	12.79	11	303	311
1TS	-3.23	13.27	10	288	297
1TS	-4.83	15.23	2	396	422
1TS	-4.47	14.60	12	312	377
1TV	13.60	1.61	10	292	422
1UE	7.48	11.30	10	288	422
1UH	6.76	10.22	10	288	422
1UJ	17.34	11.83	10	288	422
1UP	16.81	7.61	11	303	324
1UY	19.78	7.26	10	289	310
1UY	17.30	11.19	2	313	422
1VP	11.71	-0.49	2	362	422
1VP	13.57	-0.28	11	288	361
1WG	7.47	9.32	2	395	420
1WG	10.54	8.50	11	288	393
1WH	12.94	2.91	11	288	389

1WW	10.96	7.33	10	288	294
1WW	8.74	2.98	11	304	422
1XJ	10.48	21.66	10	288	291
1XJ	9.45	7.71	11	304	422
1XQ	14.32	8.25	11	299	422
1XR	12.42	11.16	10	288	319
1XR	15.28	7.37	2	332	422
1XT	10.60	7.64	10	288	316
1XT	11.58	4.87	2	326	422
1YA	9.53	-0.60	10	288	422
1YD	19.73	-9.35	11	288	342
1YD	29.45	-26.59	2	354	422
1YW	7.45	9.21	10	288	422
1ZP	10.30	2.84	10	288	422
1ZS	9.56	2.18	10	288	422
1ZV	15.72	5.16	10	289	410
1ZW	6.45	7.55	10	288	314
1ZY	18.71	5.85	10	289	421
2AA	9.76	16.14	2	384	422
2AA	10.12	12.57	11	288	383
2AI	-9.94	15.67	11	288	369
2AL	13.25	8.39	1	378	380
2AL	9.58	16.62	2	415	422
2AL	11.20	14.76	1	381	390
2AL	10.88	17.48	1	391	403
2AL	13.62	9.43	11	288	360
2AR	8.95	7.26	10	288	318
2AT	12.97	4.35	11	288	334
2AZ	16.44	10.62	11	288	363
2BE	11.00	12.52	2	401	422
2BE	12.52	6.96	11	288	399
2BJ	4.19	8.74	10	288	422
2BO	8.63	9.42	11	288	331
2BV	13.23	8.66	10	288	317
2BV	14.94	4.17	2	318	422
2CA	11.16	6.43	10	288	422
2CH	10.27	5.99	11	288	349
2CJ	11.27	2.31	10	288	422
2CT	10.47	10.58	2	387	422
2CT	11.12	6.97	11	288	386
2DA	15.56	7.91	11	306	324
2DA	15.24	10.07	2	325	422
2DB	11.65	14.21	2	404	422
2DB	12.04	9.99	11	290	392
2DC	13.86	-0.70	11	296	386

2DF	14.28	8.56	2	400	421
2DF	14.88	8.65	11	288	329
2DF	18.45	8.61	12	338	390
2DH	17.07	4.21	10	288	422
2EF	-4.05	20.40	10	288	295
2EU	13.41	2.98	10	288	316
2EW	18.25	2.29	1	384	389
2EW	12.00	6.23	10	288	309
2EW	17.50	3.50	12	322	380
2EX	11.14	2.15	10	288	422
2FR	17.35	5.31	10	288	422
2FT	11.39	9.49	11	288	360
2GK	18.53	3.17	10	288	422
3MY	17.84	3.26	10	289	423
3NH	8.72	6.04	10	288	423
3QM	-3.87	9.30	4	475	479
3QM	13.61	0.21	10	288	423
3QX	18.72	10.37	11	288	319
3QX	19.38	6.79	6	323	423
3RD	11.60	-0.68	11	288	329
3RD	24.02	-27.84	1	355	418
3RK	7.70	9.42	2	362	423
3RK	10.70	6.42	11	288	361
3RM	15.64	5.64	10	291	423
3RN	23.54	-23.75	10	290	423
3RR	13.43	3.00	10	291	423
3SI	13.13	-0.23	10	289	423
3SP	-8.83	7.04	4	467	472
3SP	18.96	5.87	10	289	423
3SS	9.32	6.36	10	292	421
3ST	2.91	9.63	11	288	411
3TR	21.30	7.11	2	348	421
5AE	15.90	3.07	10	289	423
5AU	15.80	-0.24	10	294	423
5AY	6.31	6.02	11	307	423
5BM	10.45	0.80	10	288	423
5BN	12.67	-0.06	10	288	423
5BO	16.92	6.06	11	300	423
5BS	17.16	1.47	10	288	423
5FB	11.34	5.61	10	288	423
5FC	17.41	-19.55	10	294	423
5FH	10.69	3.28	10	288	423
5FY	15.30	5.40	10	289	423
5GD	15.82	1.87	10	288	423
5GM	17.66	4.13	10	288	318

5GM	25.01	-0.48	2	331	413
5GN	15.73	8.09	10	288	423
5HC	15.30	-0.41	2	288	423
5HE	11.36	6.31	10	288	423
5HR	13.64	6.89	10	288	295
5ID	26.92	-28.71	2	417	423
5ID	21.06	-32.37	11	309	400
5IO	14.31	1.47	11	288	413
5JK	11.46	6.96	11	288	328
5JK	13.77	5.03	2	343	423

Appendix 3

List of publications in ISI-ranked journals by Chiara Scandolara

The list includes all the publications that I have co-authored during the years of my PhD. The most recent Impact Factor (IF) of each journal is reported.

Scandolara C, Rubolini D, Ambrosini R, Caprioli M, Hahn S, Liechti F, Romano A, Romano M, Sicurella B, Saino N (2014) Impact of miniaturized geolocators on barn swallow (*Hirundo rustica*) fitness traits. In press on *Journal of Avian Biology* (IF: 2.02).

Saino N, Romano M, **Scandolara C**, Rubolini D, Ambrosini R, Caprioli M, Costanzo A, Romano A (2014) Brownish, small and lousy barn swallows have greater natal dispersal propensity. *Animal Behaviour* 87: 137-146 (IF: 3.068).

Scandolara C, Caprioli M, Lardelli R, Sgarbi G, Rubolini D, Ambrosini R, Saino N (2014) Brothers and sisters are stabbing each other in the back: long-term effects of sex of siblings on barn swallow offspring. *Animal Behaviour* 87: 187-193 (IF: 3.068).

Scandolara C, Lardelli R, Sgarbi G, Caprioli M, Ambrosini R, Rubolini D, Saino N (2014). Context-, phenotype-, and kin-dependent natal dispersal of barn swallows (*Hirundo rustica*). *Behavioral Ecology* 25: 180-190 (IF: 3.216).

Saino N, Romano M, Caprioli M, Lardelli R, Micheloni P, **Scandolara C**, Rubolini D, Fasola M (2013) Molt, feathers growth rate and body condition of male and female barn swallows. *Journal of Ornithology* 154: 537–547 (IF: 1.632).

Ambrosini R, Rubolini D, Trovò P, Liberini G, Bandini M, Romano A, Sicurella BC, **Scandolara C**, Romano M, Saino N (2012) Maintenance of livestock farming may buffer population decline of the barn swallow *Hirundo rustica*. *Bird Conservational International* 22: 411–428 (IF: 1.074).

Saino N, Romano M, Caprioli M, Ambrosini A, Rubolini D, **Scandolara C**, Romano A (2012) A ptilochronological study of carry-over effects of conditions during wintering on breeding performance in the barn swallow. *Journal of Avian Biology* 43: 513–524 (IF: 2.02).

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