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General Introduction

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Population regulation in migratory birds

Theoretical background

Understanding the processes and factors underlying the distribution and abundance of birds and predicting the impact of environmental change on populations requires knowledge on population dynamics (including reproduction, mortality, dispersal, habitat use) and their temporal and spatial variation. Compared to resident bird species, migrants’ population sizes are influenced by conditions in more than one area, which in case of long-distance migrants are widely separated geographically and might differ greatly in carrying capacity (Newton 2004b, 2008). Factors operating in the wintering range might limit breeding population size, or factors operating in the breeding range might limit wintering population size, which makes understanding population regulation in migrants complex (Fretwell 1972; Sherry & Holmes 1995; Newton 2004b, 2008). Breeding numbers of migrant populations could be ‘winter-limited’, i.e. the extent or carrying capacity of non-breeding habitat leaves too few birds returning to the breeding areas to fill all breeding habitats. But breeding numbers could also be ‘summer-limited’ with more birds returning to the breeding area than this could hold, resulting in competition (density-dependent regulation) and a surplus of individuals (non-breeders). The same is true for the non-breeding areas, either too few birds arrive there to use the resources which leads to good survival, or the number of birds exceeds the carrying capacity which leads to competition and poor survival (Newton 2004b, 2008). In addition, populations can be ‘summer-limited’ through reproduction when reproductive output is too low to produce sufficient numbers to occupy all breeding or wintering habitat subsequently (Newton 2004b, 2008). Finally, a species might be winter-limited in one year or area and summer-limited in another year or area (Newton 2004b, 2008).

Population size is in equilibrium when per capita winter mortality rate (hereafter mortality) equals per capita net breeding output rate (reproduction minus breeding mortality, hereafter breeding output; Fretwell 1972; Sutherland 1996). In a situation with more or less stable breeding and wintering habitats (normal annual fluctuations in food abundance), density-dependent regulation processes keep the population size stable (Fig. 1.1A). Higher breeding output leads to more competition in winter with lower survival as a consequence, whereas lower mortality in winter leads to more competition for territories and mates in the breeding area which might result in lower breeding output. Population size of migrants is determined by the relative strengths of the density dependence acting during breeding and winter (Sutherland 1996, 1998). However, very little is known about density dependence in the non-breeding period (Goss-Custard et al. 1995), but modelling work suggests that understanding density-dependent effects is necessary to understand the population dynamics of long-distance migrants (Dolman & Sutherland 1995; Runge & Marra 2005).

Habitat (or food) loss in either breeding or non-breeding areas could lead to population declines (Fig. 1.1B,C,D; Dolman & Sutherland 1995; Sutherland 1996; Newton 2004, 2008). This is due to a decreasing carrying capacity, which is most often determined by food and competition (intra- and inter-specific) but can also be influenced by nest sites, parasitism, predation, disease, and human persecution. However, food seems to be an important factor
limiting populations during winter (Sherry et al. 2005). The consequences of habitat loss are greatest for the season in which density dependence is strongest (Sutherland 1996). If density dependence acts during a season following habitat loss in the preceding season, a ‘seasonal compensation effect’ occurs (Norris 2005). For example, reduced population size due to habitat loss in the wintering area can be (partly) compensated because the remaining individuals will have a higher breeding output at the now lower density (Norris 2005) or a higher survival in summer (Rakhimerdiev et al. 2015). The magnitude of the seasonal compensation effect depends on the relative strengths of density dependence between the seasons (Sutherland 1996). However, population equilibrium models assume that habitat is of uniform quality and fully occupied throughout, but habitat quality (food and other resources) and thus carrying capacity vary between areas. Habitat quality can have effects on physical condition and survival (Marra & Holmes 2001). The loss of high-quality habitat, compared to average-quality habitat, further decreases equilibrium population size (Norris 2005). Understanding the relation between habitat loss and population size is therefore of vital importance for conservation (Dolman & Sutherland 1995).

**Carry-over effects link individual performance across seasons**

However, events during the non-breeding period do not only influence breeding population dynamics at the population level through density-dependent survival and reproduction. They can also act on the individual level, affecting individual breeding strategies such as overall reproductive success, parental care or extra-pair copulatory behaviour (Webster & Marra 2005). These individual-based seasonal interactions, or carry-over effects, occur if events and conditions in one season or region affect populations and individuals in another (Webster & Marra 2005). Individuals carry over the effects of events and processes in one season to the next. The subsequent consequences on physical condition and arrival date could influence reproductive output and survival, thus individual performance, in a later season (Runge & Marra 2005; Harrison et al. 2011). I use the term ‘carry-over effects’ in the sense of ‘reversible state effects’ – “reversible changes in a functional trait resulting from life-history trade-offs during adulthood that affect fitness” as defined by Senner et al. (2015) and not in a broader sense of all non-lethal interactions between distinct periods of an organism’s lifetime as described in O’Connor et al. (2014). Whereas the seasonal compensation effect through density-dependent processes weakens the impact of changed conditions in one area on population size in the other area, carry-over effects reinforce the impact. The mere presence or strength of carry-over effects does not affect population size, but changing habitat quality or availability affects the proportion of individuals experiencing these carry-over effects with subsequent consequences for population size (Norris & Taylor 2006). Individual quality differences may also influence the impact that carry-over effects can have on population size (Norris & Marra 2007). Carry-over effects impact negatively on population size when mean habitat quality declines (Norris & Taylor 2006). They can be substantial if the population is limited in the season when the carry-over effects originate, thus breeding population size can be influenced by carry-over effects especially if the population is winter-limited (Runge & Marra 2005). Loss of high-quality habitat could lead to more individuals wintering in poor quality habitat which can, in addition to increased mortality, carry over to
Figure 1.1. Influence of habitat loss on population size in migrants. Population is stable when habitat in breeding and non-breeding range remains good (A), but declines if habitat deteriorates either in the breeding range (B), the non-breeding range (C), or both (D). Grey arrows depict possible ‘seasonal compensation effects’ (Norris 2005). BO = Breeding output.

delayed arrival and reduced reproductive success which consequently lowers population size (Norris 2005). The incorporation of carry-over effects in population models is important to improve predictions of how population size is affected by changing habitat quality (Norris & Taylor 2006).

Furthermore, we should not forget the migration periods that lie in-between breeding and wintering seasons. Evidence is accumulating that in migrant species, mortality during (especially spring) migration is relatively high compared to other periods of the annual cycle (Lok et al. 2013; Klaassen et al. 2014). During migration density-independent factors are
thought to be most important, but density-dependent processes might act in stopover areas for some species (Newton 2008). In addition, mortality during migration could be linked through carry-over effects of habitat quality (including competition) in the area where the individual prepared for its migratory journey.

**Migratory connectivity structures populations**
The strength of migratory connectivity, the extent to which individuals from the same breeding area spend the winter in the same non-breeding area and vice versa, might affect the ability of species to adapt to changing conditions (Webster et al. 2002). Individuals of populations with strong migratory connectivity share the same selective pressures during breeding and winter which potentially enhances local adaptation. However, strong connectivity also increases vulnerability to habitat loss if most individuals depend on a single wintering area. When migratory connectivity is strong, breeding populations can be severely affected by loss of winter habitat (Dolman & Sutherland 1995). Seasonal interactions, both on the individual and population level, also depend on the degree of migratory connectivity between seasons (Norris & Marra 2007). In reality, migratory connectivity varies largely and is not yet well understood. In many long-distance migrants in the Nearctic-Neotropical as well as the Palearctic-African migration systems, migratory connectivity seems rather low (Finch et al. 2017). High population spread might make populations more resilient when facing habitat shifts due to climate change, but in case of overall habitat loss it might lead to less individuals reaching suitable habitat (Cresswell 2014; Finch et al. 2017). This means that the loss of any non-breeding site will have a diffuse but widespread effect on many breeding populations (Finch et al. 2017). Ongoing habitat loss in breeding and non-breeding areas therefore makes it crucial to gain knowledge on migratory connectivity (Webster et al. 2002).

In conclusion, the processes and reasonings summarised above show why population regulation in migrants is complex to understand. Migrant populations are likely affected more by changes in either the breeding or the wintering area, but which area is most important might change through time and in response to annual fluctuations of conditions (Newton 2004b, 2008). Population limitation by conditions in the non-breeding areas is further complicated by the fact that many species are itinerant during winter. Therefore, not only one area has to be considered but several that might be used for different amounts of time each year or even differ between years (Newton 2004b, 2008). Deteriorating conditions at one of the staging points during the annual cycle might lead to the development of a bottleneck, which subsequently limits the population. If, however, conditions deteriorate everywhere, bottlenecks are hard to pinpoint. Since individual migrants rely on several areas in succession that are often geographically widely separated, they can suffer if any one of these areas deteriorates or is lost. Hence, they may experience multiple jeopardies during their annual cycles (Newton 2004b). Habitat loss in the breeding, non-breeding, stopover areas, or even in several of those can thus cause changes in population size (Fig. 1.1B,C,D). However, this depends on where the population is limited and the extent of habitat loss. When a population is winter-limited, with breeding carrying capacity always exceeding wintering carrying capacity (Fig. 1.2A), changes in the breeding areas have no immediate effect, or vice
Figure 1.2. Simple conceptual population model for a migratory species, in which the carrying capacity for the wintering area fluctuates strongly between years, whereas it is stable for the breeding area (A-C) or decreases over time in the breeding area (D). (A) Population is winter-limited, since carrying capacity for the breeding area is never reached. (B) Population is summer-limited, since wintering carrying capacity always exceeds breeding carrying capacity, and hence population is not determined by variation in winter conditions. (C) Population size is to a varying degree determined by winter and breeding carrying capacity. When conditions during winter are favorable, population size is limited by breeding carrying capacity. Hence the environmental effect of winter conditions levels off at better winter conditions. (D) When carrying capacity in the breeding area declines over time, the population changes from mostly winter to mostly breeding-season limited.

versa (Fig. 1.2B). If carrying capacity of one season fluctuates largely, habitat loss in the breeding areas starts to limit the population in years when wintering conditions are good, so the limiting season is different between years (Fig. 1.2C). In case of decreasing carrying capacity of one season the limitation will however change over time and a population that had been winter-limited becomes breeding-limited (Fig. 1.2D). Predicting the effects of habitat loss depends on knowledge on the strength of carry-over effects and the relative strength and functional form of density dependence within each annual cycle period which is still lacking for most species (Norris & Marra 2007). Effective monitoring schemes also need information on migratory connectivity (Norris & Marra 2007). In addition, migrant population size might also be influenced by weather and climate change. However, the impact is difficult to predict and varies temporally and spatially (Sillett et al. 2000; Bairlein & Hüppop 2004). Population regulation in migrants can only be understood if we have quantitative knowledge on carrying capacities of both winter and breeding areas, on how these carrying capacities affect year-round density-dependent mechanisms, and on how conditions experienced during one part of the annual cycle carry over to demographic rates in subsequent
periods (Norris 2005; Runge & Marra 2005; Norris & Marra 2007). This is important to
direct conservation measures effectively, but much work has still to be done to obtain direct
estimates to parametrize population models to understand and predict changes in bird
numbers (Runge & Marra 2005).

**Examples from the Palearctic-African migration system**

That is as far as the theory goes. For real populations, it is often difficult to relate population
changes to events during one of the annual cycle periods, because individuals need to be
followed through time. Therefore, most seasonal correlations are indirect: correlations
between changes in numbers and changes in conditions in the breeding or wintering areas.

In the Palearctic-African migration system, billions of birds travel annually between their
breeding and non-breeding areas (Moreau 1972; Hahn et al. 2009). In recent decades, Afro-
Palearctic migrant bird populations have been declining throughout Europe and often these
declines have been stronger than in resident or short-distance migrant species (Sanderson et
Declines and population fluctuations have been linked to Sahel rainfall patterns in West
Africa for species relying on the Sahel as wintering site, especially during the Great Drought
2009; Ockendon et al. 2014). Several Palearctic-Afrotropical migrant populations that winter
in the Sahel or rely on it for migration have been shown to fluctuate in numbers and survival
rates in relation to rainfall in the wintering areas, for example Purple Heron *Ardea purpurea*
(Den Held 1981; Cavé 1983), Sand Martin *Riparia riparia* (Bryant & Jones 1995; Szép 1995,
Robinson et al. 2008; Norman & Peach 2013), Barn Swallow *Hirundo rustica* (Moller 1989;
Robinson et al. 2008), House Martin *Delichon urbicum* (Robinson et al. 2008), Nightingale
*Luscinia megarhynchos* (Boano et al. 2004), Common Whitethroat *Sylvia communis*
(Winstanley et al. 1974; Hjort & Lindholm 1978; Bailie & Peach 1992), and Sedge Warbler
*Acrocephalus schoenobaenus* (Peach et al. 1991; Bailie & Peach 1992). White Stork *Ciconia
ciconia* populations declined and fluctuated due to reduced reproduction and reduced winter
survival related to food availability (Dalling & Schoenmakers 1987; Kanyamibwa et al.
turtur* have been shown to fluctuate with cereal production in the wintering range
(Eraud et al. 2009). More than 60 studies demonstrated the negative effects of unfavourable
ecological conditions on phenology, reproduction and survival (summarized in Zwarts et

However, these population changes were mainly observed in relation to the Great
Drought in the Sahel. Despite an increase in Sahel rainfall after the Great Drought (Nicholson
et al. 2000), many bird populations have not fully recovered or continue to decline (Zwarts
et al. 2009; Thaxter et al. 2010; Ockendon et al. 2012; Vickery et al. 2014). Whereas during the
drought period mainly species of the arid Sahel zone had declined and partially recovered
thereafter, species wintering in the more humid Guinean zone south of the Sahel have shown
steeper declines since the late 80ies (Sanderson et al. 2006; Thaxter et al. 2010; Ockendon et
al. 2012; Vickery et al. 2014). Their annual survival was generally higher than for species
wintering in the arid zone, which indicates that processes during the breeding period might
influence population declines nowadays (Johnston et al. 2016). The strength of decline differs between breeding populations, suggesting that variation in the quality of breeding habitat interacts with influences of wintering conditions (Morrison et al. 2013). It seems that some species, from being winter-limited during the Great Drought, might have become summer-limited due to habitat loss and climate change (Both et al. 2010). Even though winter rainfall might drive annual fluctuations of migrant populations, human-related habitat change is the most important factor affecting long-term trends in migrants during the breeding and especially wintering period (Vickery et al. 2014; Walther 2016). Other factors acting in the wintering areas are wetland conversion, increased fire frequency, overharvesting, persecution, poisoning, and death caused by human artefacts and disturbance (Walther 2016). Year-round, factors driving population declines of long-distance migrants apart from habitat changes due to changes in land use are illegal killing and taking, and climate-induced changes in timing of migration and breeding (Bairlein 2016).

As explained above, considering seasonal interactions is important to understand the changes in migrant numbers. In fact, some of the first studies describing wintering-condition effects on breeding populations already mentioned indications of individual carry-over effects. Not only did the population sizes decrease with less rainfall in the Sahel, but the arrival of birds in the breeding area was delayed or breeding success decreased (Dallinga & Schoenmakers 1987; Moller 1989; Szép 1995). This was not yet shown on the individual level, but only on population level, with average arrival dates being later in dryer years. Even now, direct evidence of carry-over effects observed at the individual level remains scarce. In the Nearctic-Neotropic migration system, first proof was found for American Redstarts Setophaga ruticilla in which winter habitat quality influenced arrival date and physical condition in the breeding area (Marra et al. 1998) and ultimately reproductive success (Norris et al. 2004). Black-tailed Godwits Limosa limosa islandica wintering in Britain have also been shown to arrive early when originating from higher-quality wintering sites (Gill et al. 2001). Poor conditions in the sub-Saharan wintering areas resulted in delayed arrival of individual Barn Swallows, followed by delayed breeding and a reduced frequency of second broods, as well as less offspring fledged, compared to years with favourable wintering conditions (Saino et al. 2004, 2017). White Storks wintering at southern latitudes had higher breeding success, after correcting for arrival date, than individuals wintering in less favourable conditions in the Sahel (Rotics et al. 2018). Seasonal interactions at the individual level were also found in Pied Flycatchers Ficedula hypoleuca where temperature during spring migration and stopover correlated with arrival on the breeding grounds (Both et al. 2005). However, evidence from individuals tracked over several consecutive years is still lacking.

The above examples show that migrant populations can be limited in the breeding as well as in the wintering area and that we should especially not forget about the interactions between seasons. This makes investigations more complex, but annual-cycle research is the only way to gain knowledge on bottlenecks and pinpoint conservation priorities (Marra et al. 2015). For example, Bar-tailed Godwits Limosa lapponica taymyrensis shortened their refuelling time at a spring stopover site to keep pace with advanced phenology on the breeding grounds at the cost of decreased survival, thus the stopover site becoming a bottleneck due
to changing conditions (Rakhimberdiev et al. 2018). Habitat deterioration and destruction in combination with climate change has been identified as the biggest threat to biodiversity (Travis 2003). Therefore, there is an urgent need to study population dynamics of long-distance migrants including carry-over effects, the role and location of stopover sites, migration routes and wintering areas (Bairlein 2016). Individual tracking throughout the annual cycle (Robinson et al. 2010; Bridge et al. 2011; McKinnon et al. 2013; Kays et al. 2015; López-López 2016; McKinnon & Love 2018) will help to gain detailed knowledge on species’ movements and to determine drivers of species’ declines.

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**Changes in land use in West Africa and their impact on wintering Palearctic migrants**

**Land-use changes in West Africa**

West Africa is characterized by latitudinally aligned eco-climatic zones from the north to the south, defined by the amount of rain brought north due to the Inter-tropical Convergence Zone (ITCZ). Rainy seasons are short in the north and rains increase as one goes south (Moreau 1972; Zwarts et al. 2009). South of the Sahara Desert, the savannah region is divided from north to south into the Sahel, Sudan, and Guinea Zone. These are followed by the Rainforest Zone. The Sahel, a 500 km wide belt between roughly 12° and 18°N stretching from the Atlantic coast to the Red Sea, is a semi-arid zone dominated by Acacia and Balanites bush savannah (Moreau 1972; Morel & Morel 1992; Zwarts et al. 2009). A single annual rainy season of about three months (between June and October) brings about 200–550 mm of rain which varies highly between years (Moreau 1972; Morel & Morel 1992; Zwarts et al. 2009; Walther 2016). Periods of droughts have increased since 1969 (Zwarts et al. 2009). After the severe drought (Great Drought or Sahel Drought) between 1972 and 1992, rainfall has increased, but is still below or just above the long-term average of the 20th century (Nicholson et al. 2000; Zwarts et al. 2009; Walther 2016). The adverse effects of these periods are intensified by rapid man-made changes in land use and vegetation cover in the Sahel and other eco-climatic zones. In West Africa, nearly 90% of the original moist forest has disappeared and the remaining parts are highly fragmented and degraded (Zwarts et al. 2009). In Senegal for example, 90% of Acacia nilotica woodland disappeared between 1954 and 1986 (Morel & Morel 1992) and 41% of forest between 1965 and 2000 (Tappan et al. 2004). Tree density in a forest reserve in northern Nigeria decreased by 82% between 1993 and 2001 (Cresswell et al. 2007). Habitat loss was caused in these cases by clearance for fuel wood, grazing and conversion to intensive farmland (Wilson & Cresswell 2006). The agricultural area in sub-Saharan Africa increased by 57% between 1975 and 2000 to nearly 340 million hectares at the expense of forest (decrease 16%) and natural non-forest vegetation (5%) and an increase of bare area by 15% (Brink & Eva 2009). The increase in area used for agriculture was accompanied by an increase in fertilizer and pesticide use (FAOSTAT database of the UN’s Food and Agricultural Organisation: www.fao.org/faostat). At the same time, livestock densities have increased immensely, with numbers doubling in only two decades after the dry year 1984 to 150 million cattle and 300 million sheep and goats.
(Zwarts et al. 2009). The Sahel region, home to 31 million people in 1950 and more than 100 million in 2013, has one of the world’s highest growth rates, with the human population doubling every 20 years resulting in possibly 340 million people by 2050 (Potts et al. 2013). Global food demand is predicted to double by 2050, which will lead to further habitat destruction and intensification of agriculture especially in sub-Saharan Africa (Tilman et al. 2001, 2002). The recent re-greening of the Sahel, maybe positive from the viewpoint of agricultural productivity and resilience, is also called ‘green desertification’ of the Sahel (Herrmann et al. 2014) since the human-dominated cultural landscape is characterized by intensive agriculture and overstocked livestock herds as well as degraded areas with hardly any large wildlife left (Walther 2016). The ecosystems of the Sahel with their impoverished biodiversity state are well on the way to becoming another agricultural desert of the world (Green et al. 2005; Walther 2016).

Impact of land-use changes in West Africa on birds
As described above, breeding populations of many European long-distance migrants have declined during the last decades. The Sahel drought was not the only and most important long-term cause of the population declines in migrants. The human-induced rapid land-use change, resulting in biodiversity loss, especially of woody vegetation and wetlands, likely caused these declines (Walther 2016). Increased use of pesticides might also influence migrants directly (Mullie & Keith 1993). Declines are not only especially visible in Palearctic migrants that spend part or the entire time of their non-breeding season in the Sahel, but also in large raptors, vultures and gamebirds (Walther 2016). The observed tremendous declines in raptors and vultures of 83% in the Sudan zone between 1969-73 and 2003/2004 (Thiollay 2006a) and in the northern Sahel (Thiollay 2006b) were thus not only attributed to habitat change but also to increased human pressure (hunting, poisoning, disturbance). At the beginning of the 21st century, most large raptors and vultures were generally almost only found in protected areas (Thiollay 2006a, c, 2007).

Detailed field studies in the wintering areas are urgently needed to improve our knowledge related to these declines (Vickery et al. 2014; Adams et al. 2014). In 2014, only 20 papers related migrant land-bird population declines to land-use changes in the Sahel having collected data in the Sahel (Adams et al. 2014). The most important factors reported in those were the loss of wetlands and wooded savannah (Adams et al. 2014).

It has been suggested that the loss of forest has little effect on migrants because the majority of species favours open habitats (Moreau 1970; Morel & Morel 1992), thus they might not be negatively affected by changes of forest into secondary ‘derived savannahs’ (Newton 2008). There are only few studies that have investigated habitat use of migrants during their stay until now (Morel & Morel 1992; Vickery et al. 1999; Wilson & Cresswell 2006), thus it remains difficult to predict effects of habitat degradation on densities and distribution of migrants. However, densities of Palearctic migrants as well as of Afrotropical residents were higher in woodland habitats compared to agricultural areas or savannahs, indicating that loss of woodland habitat might influence both (Wilson & Cresswell 2010a). Unfortunately, there are also few studies on the densities of Afrotropical species (Morel 1973; Jones et al. 1996; Vickery et al. 1999). Deforestation (82% in the eight-year study
period) in the protected area of Watacul Forest Reserve in northern Nigeria caused a decrease in density, number of species and diversity (Cresswell et al. 2007). But stabilization on this lower level occurred in the following five-year period when habitat hardly changed anymore (Stevens et al. 2010). Concerning Palearctic migrants, deforestation had a negative impact on Common Whitethroat and Subalpine Warbler Sylvia cantillans, but positive effects on Bonelli’s Warbler Phylloscopus bonelli, Yellow Wagtail Motacilla flava (Cresswell et al. 2007), Northern Wheatear Oenanthe oenanthe (Cresswell et al. 2007; Wilson & Cresswell 2010b), Whinchat Saxicola rubetra (Hulme & Cresswell 2012; Blackburn & Cresswell 2015), and Lanius shrike species (Moreau 1970). Whinchats, for example, seem to profit from secondary open landscapes due to the increase of agriculture and have been shown not to be winter-limited (Hulme & Cresswell 2012; Blackburn & Cresswell 2016a, b). Overall, Palearctic warbler species seem to be quite robust to habitat degradation, occurring at relatively constant densities across a range of habitats, but severe habitat loss in combination with drought might change this (Wilson & Cresswell 2006). However, for Wood Warbler Phylloscopus sibilatrix it has been shown that its specific habitat preferences make the species prone to be winter-limited due to a decreasing availability of suitable habitat (Mallord et al. 2016). This might also be true for habitat specialists which depend on the availability of few habitat types, as found in Aquatic Warbler Acrocephalus paludicola (Arbeiter & Tegetmeyer 2011). On the contrary, not only deforestation but all habitat changes will impact Afrotropical species since they also use these habitats for breeding (Cresswell et al. 2007; Wilson & Cresswell 2010a).

Even in open landscapes and farmland, trees and shrubs are important for migrants and Afrotropical species (Jones et al. 1996; Douglas et al. 2014). This has also been found for species preferring very open habitats, such as Northern Wheatear (Wilson & Cresswell 2010b). On the large scale of the western Sahel, Palearctic migrants as well as African species are highly selective in their choice of tree species, with highest densities found in berry-carrying Salvadora persica shrubs and indigenous thorny arthropod-rich (often Acacia) tree species (Zwarts et al. 2015). Thus, birds do not profit from the ‘re-greening’ of the Sahel with non-native tree species like Neem and Eucalyptus which were and are planted on a large scale (Zwarts et al. 2009).

Many of the Afro-Palearctic migrants occur at relatively low densities on the land of rural people, which makes conservation difficult. Hence, the mere establishment of protected areas will not solve the problem for most species, as reserves will contain an insufficient part of the whole wintering population. Instead, their conservation demands a landscape-scale approach and the success is inextricably linked to livelihood security of Sahelian people (Söderström et al. 2003; Adams et al. 2014). The importance of agricultural landscapes for open-habitat species is often overlooked in conservation approaches focusing on natural habitats (Wright et al. 2012). However, the effects of habitat degradation on future density and distribution of migrants are largely unknown due to few baseline data on habitat use. Unfortunately, field studies in biodiversity research which are needed to improve conservation are hampered by human activity such as conflicts in many areas (Brito et al. 2014).
Changes in agricultural practices in Europe and their impact on breeding birds

A total of 25% of Europe’s land is covered by arable land and permanent crops, and another 17% by permanent pastures and mixed mosaics (European Environment Agency 2017). In Europe, agricultural practices have changed rapidly during the last decades from small-scale agriculture towards industrial farming. The invention of artificial fertilizers increased productivity tremendously (Tilman et al. 2002), and the memory of hunger during and after the second world war drove the European Union to raise productivity even further. The European Common Agricultural Policy (CAP) was initially leading these changes in western European countries, and more recently is changing the farming practices in eastern European countries after they joined the European Union. Recent changes in agricultural practices towards increasing yields included: increasing mechanisation leading to larger farms, increasing specialization of farms in either arable crops or livestock reducing habitat diversity at the landscape scale, increased field size through removal of hedgerows, increased use of pesticides and inorganic fertilizers, increased level of autumn sowing of crops reducing the amount of stubble, and less wastage of grains during harvest (Donald et al. 2001; Robinson & Sutherland 2002; Benton et al. 2003; Newton 2004a). This industrialization and intensification dramatically changed and homogenized the landscape.

Through this increased landscape homogeneity, strongly interacting multivariate effects of agricultural practices cause the current biodiversity decline (Benton et al. 2003). Farmland birds in Europe have declined steeply during the last decades and in contrast to the African situation described above, it is well documented that these declines are caused by the intensification of agriculture (Chamberlain et al. 2000; Donald et al. 2001; Guerrero et al. 2012). The declines of farmland birds were stronger than in woodland species in England between 1967 and 2006, but strongest in the 70ies and 80ies (Thaxter et al. 2010). During this period, the intensification of agricultural practices led to large-scale land-use changes, followed by reduced food for farmland birds, reducing their survival and productivity (Chamberlain et al. 2000). Population decline of farmland passerine seed-eaters is strongly related to decreased food availability in winter and changes in survival (Robinson & Sutherland 2002). Changes in grassland systems are as substantial as in arable farming, with a high proportion of grassland managed intensively, doubled use of inorganic nitrogen, a switch from hay to silage, increased stocking densities, and transformation from structurally diverse and species-rich swards to dense, fast-growing and structurally uniform swards which leads to deteriorated nesting and wintering habitat, nest destruction and decreased food availability of seeds and invertebrates (Vickery et al. 2001).

To counteract biodiversity loss, agri-environment schemes (AES) were introduced in EU policy in 1992. However, their effectiveness for biodiversity is often poorly monitored, and in cases where it has been monitored the results were rather poor, or even undetectable (Kleijn et al. 2001, 2004, 2006; Bradbury & Allen 2003; Kleijn & Sutherland 2003; Pe’er et al. 2014). The success of AES is mixed or meagre due to broad and shallow approaches (Kleijn et al. 2006). For example, no increase in seed-eaters has been documented despite the widespread introduction of set-aside in 1992, because the management of the AES limits the extent of
weed seeds (Robinson & Sutherland 2002). Despite all efforts and investments during the last CAP periods, farmland birds are still in steep decline (Pe’er et al. 2014). Nevertheless, there are some success stories where AES did lead to the partial recovery of a species. The best example is the Cirl Bunting Emberiza cirlus in southern England which increased by 83% between 1992 and 1998 due to weed-rich winter stubbles implemented for the species (Peach et al. 2001) and even exceeded one thousand pairs in 2016 (Jeoffs et al. 2018). This example shows that targeted management proves to be most successful (Pywell et al. 2012), which was also the case for Corn Buntings Emberiza calandra (Perkins et al. 2011). On a larger scale, farmland management at two demonstration farms in the UK led to an increase of the carrying capacity for a wide range of farmland birds (Aebischer et al. 2016). Wildlife-friendly farming, involving the close integration of conservation and extensive farming practices, might be a better solution to address biodiversity loss in agricultural landscapes than single AES measures (Pywell et al. 2012).

Species in double jeopardy
Farming is a major current and likely future threat to threatened and near-threatened bird species in the developed and especially in the developing world (Green et al. 2005). More species of long-distance migrants wintering in savannah and wooded savannah associated with farmland and steppe in the breeding range declined (47%) than savannah species not breeding in farmland and steppe (23%) (Zwarts et al. 2009). An example of such a species in double jeopardy is the Montagu’s Harrier Circus pygargus, topic of my thesis, for which habitat has deteriorated on the breeding grounds due to intensification of agriculture, and conditions have deteriorated on the wintering grounds due to changes in land use in combination with intensification of agriculture.

Introduction to the study system
Montagu’s Harrier
The Montagu’s Harrier is a long-distance migratory raptor with a southwest-Palearctic breeding distribution and an Afrotropical/Indomalayan wintering distribution (Ferguson-Lees & Christie 2001). The European population is estimated by BirdLife International at 54,500–92,200 breeding pairs which represent only 41% of the global population (BirdLife International 2016). The global estimate of 266,000 to 499,000 mature individuals (BirdLife International 2016) is thus largely based on highly uncertain numbers of breeding pairs in Russia. Ferguson-Lees & Christie (2001), however, estimated the global population at 60,000–71,000 breeding pairs (thus 120,000–142,000 mature individuals which is half of the minimum estimate of BirdLife International) and the European population at 9,800–15,000 breeding pairs. The BirdLife International estimates result in the IUCN categorizing the species as Least Concern (BirdLife International 2016), even though it is declining and re-listed in many European countries including the strongholds of the species in France and Spain. In Spain, hosting an estimated population of 6,000–7,300 pairs, the species has been reassessed as Vulnerable after the national census in 2006 indicated decreasing trends
(SEO/BirdLife 2010). In France, hosting an estimated 4,500 (3,900–5,100) breeding pairs (Millon et al. 2004), the species is classified as Near Threatened on the national red list with a decreasing trend (IUCN France et al. 2016). In France, there is evidence of a slight decline based on demographic models (survival and fecundity estimated at the national level), the national raptor breeding survey (decline of 14% over 10 years), and intensively monitored sites (A. Millon pers. comm.). Poland hosts an estimated 3,400 (2,700–4,300) breeding pairs (Królikowska et al. 2017) but the population decreased at an annual rate of 8% between 2007 and 2012 (Krupiński et al. 2015). The species is also categorized as Endangered on the Danish red list of threatened species (Wind & Pihl 2004) as well as on the German red list (Grüneberg et al. 2015), and even as Critically Endangered on the Dutch red list (van Kleunen et al. 2017).

In recent times, Montagu’s Harriers have shifted from breeding in natural habitats like dunes and moors towards breeding in agricultural crops all over Europe. This makes the species dependent on protection measures, as chicks often do not fledge before harvesting of the crop (Arroyo et al. 2002). In addition, food abundance might limit breeding populations which can be seen for example in the extreme dependence of some populations on a single main prey species. In the Netherlands, Montagu’s Harriers strongly rely on the Common Vole Microtus arvalis with laying date, clutch size and annual population growth rate positively related to vole abundance (Koks et al. 2007). Population fluctuations in France have also been shown to be related to vole abundance (Millon & Bretagnolle 2008). This dependence on small mammals is related to the low abundance of alternative prey species, which is mainly found in northern European agricultural landscapes (Terraube & Arroyo 2011). In general, birds are the main prey of Montagu’s Harriers in most of its distribution range and diet is much more diverse in landscapes with higher availability of alternative prey (Terraube & Arroyo 2011).

Until recently, not much was known about migration routes and wintering areas of Montagu’s Harriers. Satellite tracking of adults, starting in the Netherlands in 2005 and spreading from the UK in the west to eastern Belarus in the meanwhile, revealed the most important routes for the northern European breeding population and their wintering areas (Trierweiler et al. 2007, 2014; Limiñana et al. 2012c). Individuals from western breeding populations (Netherlands, Denmark, north-western Germany) migrate mainly on a western route via Spain (78%) and to a smaller extent on a central route via Italy (22%). In spring they return on the same routes. Individuals from central breeding populations (northeastern Germany) use the Italian route or a more eastern route via Greece in autumn and spring. Individuals from eastern European breeding areas (eastern Poland, Belarus) migrate on the eastern route in autumn and return mostly via the central route (Trierweiler et al. 2014). Important stopover areas are found in northern Africa, especially in spring (Trierweiler et al. 2014).

During winter, Montagu’s Harriers spend about six months in the Sahel (Trierweiler & Koks 2009). Satellite tracking has revealed that they are itinerant and use on average four distinct wintering sites that are located progressively further south and to which individuals are site-faithful in consecutive years (Trierweiler et al. 2013). Consecutive wintering sites are on average 200 km apart and Trierweiler et al. (2013) proposed that these mid-winter
movements are related to grasshopper availability. Montagu’s Harriers prefer open landscapes with mosaics of savannah and cropland (Limíñana et al. 2012c; Trierweiler et al. 2013; Augiron et al. 2015). In winter, Montagu’s Harriers are acridivorous and mainly feed on local grasshopper species (Mullié 2009; Trierweiler & Koks 2009; Mullié & Guèye 2010; Trierweiler et al. 2013). During the dry season, grasshopper species with diapausing adults are most abundant. Adult grasshoppers are only present from mid-October onwards, and are progressively depleted during the season by predation (Mullié 2009; Mullié & Guèye 2010). In Niger, grasshoppers were most abundant in areas with relatively low (0.17–0.27) vegetation greenness (Normalized Difference Vegetation Index - NDVI). Harriers stayed within this range of greenness values indicative of high grasshopper abundance by moving to consecutive sites following a “green belt” of vegetation that hosts highest grasshopper numbers (Trierweiler et al. 2013). Montagu’s Harriers declined significantly between 1969–73 and 2003/2004 in their Sahelian wintering range by 73% outside protected areas and 56% inside protected areas (Thiollay 2006a).

Study areas
We studied Montagu’s Harriers from north-western European breeding populations. The main study area is the Dutch province of Groningen with a small, but well-studied population of about 40 breeding pairs. Whereas the Dutch population was estimated to have 500–1000 breeding pairs in the first decades of the 20th century (Bijlsma et al. 2001), at the end of the 1980ies, the species went nearly extinct with only few breeding pairs remaining in the Netherlands (Zijlstra & Hustings 1992). However, between 1988 and 1992 the large-scale introduction of fallow land in the eastern part of the province of Groningen due to wheat overproduction led to the establishment of a growing population of Montagu’s Harriers. The first two couples bred in 1990 and already 29 breeding pairs were found in 1993 (Koks et al. 2007). The harriers bred in large cereal or alfalfa *Medicago sativa* fields using the vast fallows to forage, mainly on Common Vole. Because the population in East-Groningen started to decrease again after the fallow regulation had ended, agri-environment schemes (AES) were introduced from 1997 onwards. This led to a further increase and stabilization of the breeding population ever since (Koks et al. 2007). Nowadays, the Netherlands host around 50 breeding pairs in total, with East-Groningen remaining the core breeding area and some couples in the north of the province and in the provinces of Flevoland, Friesland and sometimes Drenthe.

In addition, we have long-lasting collaborations with Danish and French colleagues, and data of birds tracked from these populations are included in several chapters of this thesis. In Denmark, the breeding population, mainly found in southwestern Jutland, consists of 20–30 breeding pairs and has been monitored closely for more than two decades through a national programme run by DOF-BirdLife Denmark (Rasmussen et al. 2018). In France, data originates from a breeding population in the south of Deux-Sèvres, well-studied by CEBC-CNRS since 1995. The population consists of 30–100 pairs depending on vole abundance (Millon & Bretagnolle 2008).

Fieldwork in the West African wintering areas was conducted at five sites in Senegal. The climate in this region is characterized by a wet season from June to October followed by a dry
season from November to May. Mean annual rainfall in Kaolack (14.15°N 16.08°W) since 1919 was 709 mm, but 647 mm during the last 20 years. The main study site was the area of Khelcom, also known as Mbégué (14.44–14.74°N and 15.42–15.64°W, ca. 55,000 ha) which is the most important known wintering area of Montagu’s Harriers in West Africa, harbouring over 5,000 individuals (Mullié & Guéye 2010; Augiron et al. 2015). In Khelcom, individual roosts support between several hundred up to 4,000 harriers (January 2015). This area, in the Mbégué Sylvo-pastoral Reserve which has been gradually deforested since 1991, nowadays consists of a mosaic of herbaceous savannah, fallow land and cropland (mainly groundnut Arachis hypogaea and millet Pennicetum glaucum; for a detailed description see Mullié & Guéye (2010)). The relatively high percentage of fallow land created a temporarily ideal habitat for wintering harriers and hosts high densities of grasshoppers (Mullié 2009). The second important study site was near Diofior in the region of Fatick (14.15–14.28°N and 16.57–16.66°W), at the edge of the Sine Saloum delta. This region, known for its salt production, is dominated by deltaic flats where wetlands bordered by halophytic vegetation are interspersed with ridges covered by shrubby savannah vegetation. The flats and wetlands dry up during the dry season leaving vast areas of bare salty sand flats, or tann. Agriculture is limited to upper and less salty soils surrounding the delta region. Harrier roosts in this area were much smaller, supporting between 50 and 300 birds, with several small roosts being located at distances of about 10 km. Our other three study sites were located near Nioro du Rip (13.85°N 15.69°W), Kaffrine (14.05°N 15.39°W), and Payama (13.65°N 15.57°W). The landscape of these more southwestern sites is characterized by low plateaus separated by wide, shallow depressions (Tappan et al. 2000). The areas around Nioro du Rip and Kaffrine are dominated by agriculture, mainly groundnut and millet production, where little bushland or fallow land remains. The landscape in the area near Payama, the southernmost site close to the border with the Gambia, is much less open and characterized by laterite plateaus alternated with dense woody vegetation and some agriculture. In all those three areas, smaller roosts with up to 50 birds were observed.

Approach
Throughout this thesis, I used state-of-the-art tracking devices in combination with traditional ecological fieldwork and remote sensing data. Tracking birds individually has improved our understanding of bird movements and behaviour considerably. Montagu’s Harriers were followed by satellite telemetry using 9.5–12 g solar-powered satellite transmitters (PTT-100, Microwave Telemetry Inc.) and GPS telemetry using 12 g solar-powered UvA-BiTS GPS trackers (Bouten et al. 2013). Tracking data were combined with data on prey abundance (vole counts in the Dutch breeding area; grasshopper counts at the African wintering sites). In addition, I used remote sensing data to investigate the wintering ecology of Montagu’s Harriers over the whole of West Africa using NDVI and the GlobCover land use map.
Outline of the thesis

As Montagu’s Harriers spend about half of their annual cycle on their African wintering grounds and wintering conditions might influence their populations through survival and carry-over effects, this thesis starts from an African perspective. Chapter 2 gives a detailed description of site use throughout the winter in relation to varying annual environmental conditions. Using a large tracking dataset, we describe movement patterns between sites, habitat use and home ranges and activity at different sites and relate this to environmental conditions using NDVI remotely sensed data.

Chapter 3 zooms in on the last wintering site harriers use before departing on spring migration. We explore if environmental conditions deteriorate during their stay and how Montagu’s Harriers cope with Moreau’s Paradox. This is investigated by combining field data collected at wintering sites in Senegal with remotely sensed environmental data (NDVI) and GPS-tracking data.

In chapter 4, a case of an over-summering male Montagu’s Harrier in Africa is described in detail. We relate the movements of the bird to environmental data (NDVI) to investigate if his stay is related to weather conditions during the winter or other factors.

After the first three chapters covering the winter period, chapter 5 gives a circannual perspective on daily and total flight distances of Montagu’s Harriers. Using GPS-tracked individuals from breeding areas in France, The Netherlands and Denmark, we calculate annual distances travelled by these birds and study how the distances covered are divided over the four annual-cycle periods.

Going to the breeding period, chapter 6 describes the variation in activity and home range size of male Montagu’s Harriers in the main Dutch breeding area. We relate activity (hours flying) and home range size to habitat use and describe their relation to food abundance.

A novel AES for Montagu’s Harriers is described and tested in chapter 7. Current AES, such as field margins that aim to improve foraging conditions (i.e. increase vole densities) for harriers, are inefficient, as prey are difficult to capture in tall set-aside habitat. ‘Birdfields’ combine strips of set-aside to boost vole numbers and strips of alfalfa, as voles are accessible after alfalfa has been harvested. We describe in detail how GPS-tracked harriers make use of this novel AES.

Finally, in chapter 8, the synthesis, I summarize and reflect on the findings of this thesis. An update on mortality rates during the four annual-cycle periods helps to point out future directives of research that are needed to further improve our understanding of population dynamics of Montagu’s Harriers and their conservation.