Almut E. Schlaich

Migrants in double jeopardy

Ecology of Montagu's Harriers on breeding and wintering grounds

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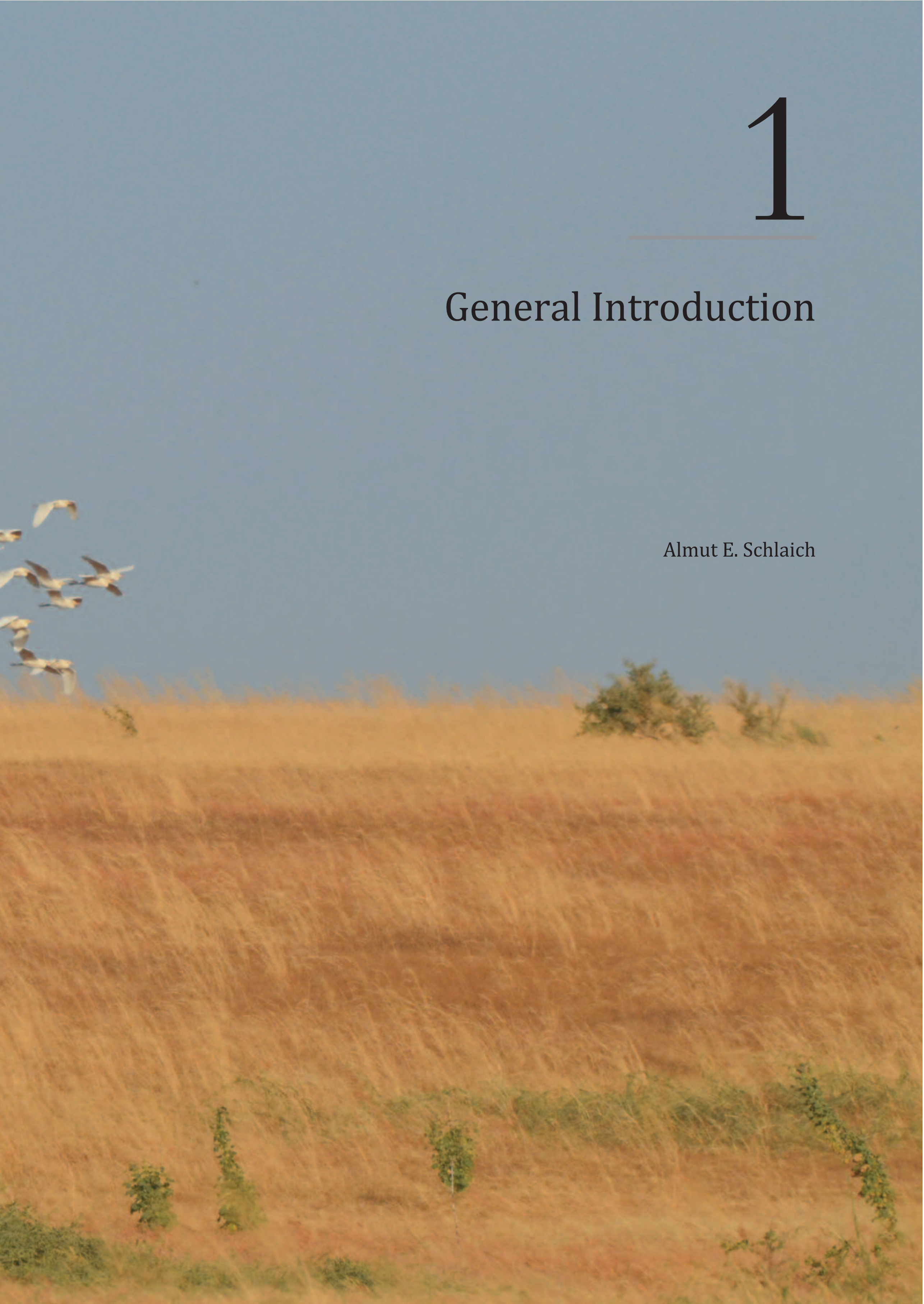

Population regulation in migratory birds

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 (Rakhimberdiev *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

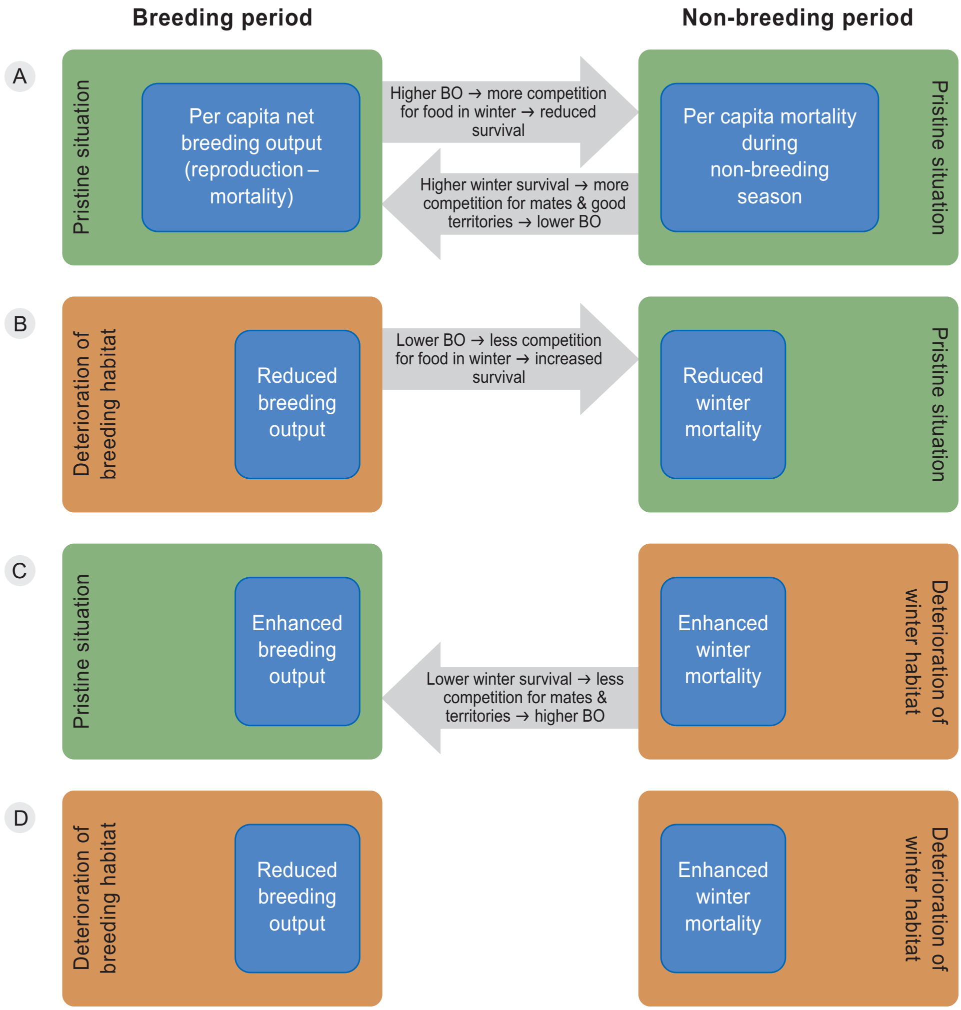

Figure 1.1. Influence of habitat loss on population size in migrants. Population is stable when habitat in breeding and non-breeding range remains good (**A**), but declines if habitat deteriorates either in the breeding range (**B**), the non-breeding range (**C**), or both (**D**). Grey arrows depict 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

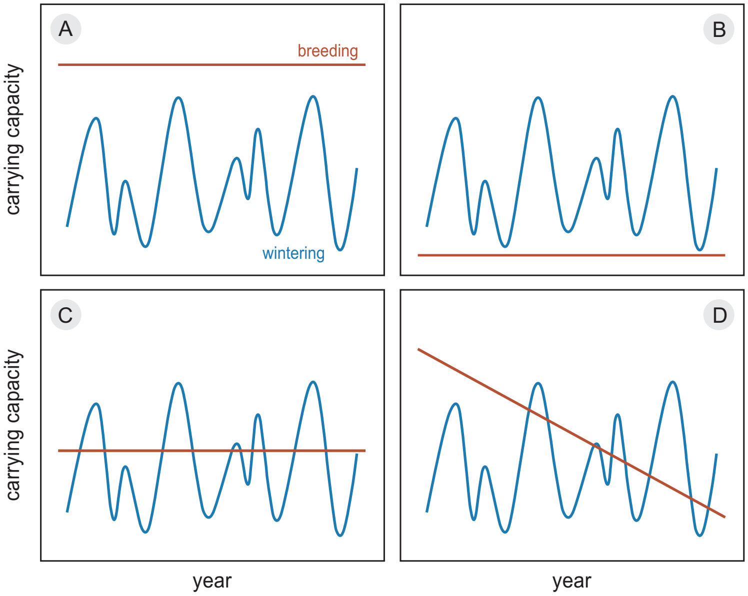

Figure 1.2. Simple conceptual population model for a migratory species, in which the carrying capacity for the wintering area fluctuates strongly between years, whereas it is stable for the breeding area (A-C) or decreases over time in the breeding area (D). (**A**) Population is winter-limited, since 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 al.* 2006; Heldbjerg & Fox 2008; Zwarts *et al.* 2009; Thaxter *et al.* 2010; Vickery *et al.* 2014). 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 in the Sahel between 1972 and 1992 (Baillie & Peach 1992; Marchant 1992; Zwarts *et al.* 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; Baillie & Peach 1992), and Sedge Warbler *Acrocephalus schoenobaenus* (Peach *et al.* 1991; Baillie & Peach 1992). White Stork *Ciconia ciconia* populations declined and fluctuated due to reduced reproduction and reduced winter survival related to food availability (Dallinga & Schoenmakers 1987; Kanyamibwa *et al.* 1990, 1993; Schaub *et al.* 2005). Annual survival rates in granivorous Turtle Doves *Streptopelia 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 al.* 2009; Vickery *et al.* 2014).

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.

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 Watucal 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 practises 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 practises 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 practises 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 practises 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 (Jeffs *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 practises, 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 red-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 (UICN 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 (north-eastern 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 (Limiñana *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 & Guèye 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 & Guèye (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.

2

On the wintering ecology of Montagu's Harriers in West Africa: a detailed description of site use throughout the winter in relation to varying annual environmental conditions

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Abstract

Winter is the longest annual cycle period for many long-distance migrants, but research on wintering ecology and movement patterns remains still limited compared to the breeding season or migrations. However, wintering conditions might influence bird populations through individual survival and carry-over effects. It is therefore important to deepen our knowledge to understand population declines and advance conservation efforts. In the Palearctic-Afrotropical migration system, many species have been shown to perform intra-tropical movements, itinerancy being their wintering strategy. We tracked 125 adult Montagu's Harriers *Circus pygargus* from western European breeding populations between 2005 and 2018 using satellite and GPS tags. In total, data on 129 complete wintering seasons were gathered, including 33 individuals that were followed in two or more seasons. Montagu's Harriers were itinerant, using on average three distinct wintering sites to which they showed high site fidelity between years. First sites, used for about one month after arrival, lay in the northern Sahel and were mainly dominated by natural and sparse vegetation. Intermediate and last sites, laying in general further south in the Sahel, were mainly dominated by agricultural and natural habitats. Harriers selected sites with higher habitat diversity compared to random sites. Home range size was largest and activity highest at last sites and higher for individuals wintering in drier areas. For individuals tracked in multiple seasons, we showed that home range size did not depend on vegetation greenness. However, birds flew more kilometres at the same site in drier years compared to greener years. The timing of intra-tropical movements was also adjusted to local environmental conditions, with individuals staying longer and departing earlier from first sites in drier years and arriving earlier at last sites in greener years. This demonstrates that individuals have no fixed time schedules but show plastic behaviour in response to environmental conditions.

Introduction

Most long-distance migrants spend more than half of their annual cycle outside their breeding areas (Newton 2008). In recent years, migratory routes and flight strategies of many species have been described in great detail, thanks to ever smaller and smarter tracking devices (Robinson *et al.* 2010; Bridge *et al.* 2011; McKinnon *et al.* 2013; Kays *et al.* 2015; López-López 2016; McKinnon & Love 2018). Behaviour and ecology of long-distance migrants during the wintering period, however, have received much less attention. This is a serious omission, since many species reside here for the longest annual cycle period and wintering conditions can have carry-over effects to subsequent seasons (Marra *et al.* 1998; Norris & Marra 2007; Studds & Marra 2011) as well as influence survival (Zwarts *et al.* 2009; Klaassen *et al.* 2014).

Many long-distance migrants wintering in Africa and breeding in Europe have declined during the past half century (Sanderson *et al.* 2006; Zwarts *et al.* 2009; Vickery *et al.* 2014). Especially for species wintering in the Sahel, these declines have been associated with rainfall conditions (Baillie & Peach 1992; Szép 1995; Zwarts *et al.* 2009), but also with changes in human land use (Zwarts *et al.* 2015). Whereas some species wintering in the Sahel have shown some recovery after the severe droughts of the '70 and '80's, their numbers often have not reached the pre-drought levels. Recent monitoring data of long-distance migrants in Europe show that species occupying the more southern humid habitats have declined in recent years (Ockendon *et al.* 2012). Despite these general patterns pointing at wintering conditions impacting on breeding populations, we know relatively little about how ecological conditions in Africa do affect behaviour and demography of European breeding birds.

Different movement strategies have been described for long-distance migrants during the non-breeding season. A strategy of winter residence, with birds remaining on a single territory throughout the winter, appears to be relatively uncommon (e.g. Osprey *Pandion haliaetus* (Kjellén *et al.* 1997; Alerstam *et al.* 2006), Common Redstart *Phoenicurus phoenicurus* (Kristensen *et al.* 2013), Northern Wheatear *Oenanthe oenanthe* (Schmaljohann *et al.* 2012), Pied Flycatcher *Ficedula hypoleuca* (Salewski *et al.* 2002; Ouwehand *et al.* 2016)). Most species seem to perform intra-tropical movements in the course of the winter. The strategy of moving with the Inter-Tropical Convergence Zone (ITCZ), called 'itinerancy' by Moreau (1972), is believed to be a strategy to track spatiotemporal variation in resources throughout the winter (Moreau 1972; Thorup *et al.* 2017). Itinerancy seems to be a common wintering strategy in Palearctic migrants wintering in Africa. First evidence came from field research at the wintering grounds, e.g. water birds that stay just south of the Sahara after their crossing until pools dry up and they have to move south (Moreau 1972) or Willow Warblers *Phylloscopus trochilus* arriving only in the first half of November in northern Ivory Coast and disappearing from the area for 4–6 weeks in January/February (Salewski *et al.* 2002), which suggested that they use other wintering sites before and afterwards. In the meanwhile, there is much more proof for itinerancy due to an increased amount of species being tracked year-round. Intra-tropical movements can be exhibited on a small scale within the northern Sahel and Sudan savannahs (e.g. Turtle Dove *Streptopelia turtur* (Eraud *et al.* 2013), Tawny Pipit *Anthus campestris* (Briedis *et al.* 2016)), or further south into the Guinean and derived savannahs and adjacent rain forest zone (e.g. Common Nightingale *Luscinia megarhynchos* (Hahn *et al.* 2014), Great Reed Warbler *Acrocephalus arundinaceus* (Hedenström *et al.* 1993; Lemke *et al.* 2013; Koleček *et al.* 2018), Willow Warbler (Lerche-Jørgensen *et al.* 2017)), but can also cover large distances up to thousands of kilometres even crossing the equator. These larger movements are often referred to as second leg of migration. The latter is found in many species that first profit from the food abundance at the end of the rainy season in the Sahel (Morel 1973), but then move on to more southernly vegetation zones as the Sahel gets dryer during the winter (e.g. Great Snipe *Gallinago media* (Lindström *et al.* 2016), Common Cuckoo *Cuculus canorus* (Willemoes *et al.* 2014; Thorup *et al.* 2017), European Nightjar *Caprimulges europaeus* (Norevik *et al.* 2017), Pallid Swift *Apus pallidus* (Norevik *et al.* 2018), Common Swift *Apus apus* (Åkesson *et al.* 2012), European Roller *Coracias garrulus* (Finch *et al.* 2015), Thrush Nightingale *Luscinia luscini*a (Stach *et al.* 2012; Thorup *et al.* 2017), Garden Warbler *Sylvia borin* (Ottosson *et al.* 2005), Red-backed Shrike *Lanius collurio* (Tøttrup *et al.* 2012b, 2017; Thorup *et al.* 2017)). Even though migrants follow seasonal changes in food availability, this does not mean that the birds are continuously on the move. On the contrary, all species for which detailed tracking shed light on their intra-tropical movements use multiple distinct non-breeding residency sites (hereafter wintering sites) to which many show site fidelity between years. Although it is well-established how a strategy of itinerancy allows migrants to profit from ephemeral resources, we lack a more detailed understanding on how individual sites are used and the factors steering the timing of movements between sites.

A species for which migration and wintering strategies have been studied notably extensively is the Montagu's Harrier *Circus pygargus*. Montagu's Harriers are long-distance migratory raptors with a southwest-Palaearctic breeding distribution and an Afrotropical/Indomalayan wintering distribution (Ferguson-Lees & Christie 2001). Tracking of European breeding birds has revealed that they migrate via Spain, Italy or Greece and winter in the Western Sahel (Limiñana *et al.* 2012c; Trierweiler *et al.* 2014) where they spend more than six months on their wintering grounds (Trierweiler & Koks 2009; Schlaich *et al.* 2017a). They arrive in the Sahel at the end of the wet season, and wintering conditions progressively get dryer during their stay (Schlaich *et al.* 2016). Being itinerant, they use on average four different distinct wintering sites that are located progressively further southwards and to which individuals show site fidelity between years (Trierweiler *et al.* 2013). Consecutive wintering sites are around 200 km apart and home range size calculated from satellite tracking data at wintering sites was on average 200 km^2 (Trierweiler *et al.* 2013). Preferred habitat types of harriers during winter are mosaics of savannah and cropland in open landscapes (Limiñana *et al.* 2012c; Trierweiler *et al.* 2013; Augiron *et al.* 2015). Local grasshopper species are the main prey for Montagu's Harriers during winter (Mullié 2009; Trierweiler & Koks 2009; Mullié & Guèye 2010; Trierweiler *et al.* 2013) and Trierweiler *et al.* (2013) proposed that mid-winter movements are related to grasshopper availability. They found that in the field, grasshoppers were most abundant in areas with relatively low vegetation greenness (Normalized Difference Vegetation Index (NDVI) values 0.17–0.27). By moving between different sites during the course of the winter, harriers manage to stay within this range of NDVI values indicative for higher grasshopper numbers. This suggests that harriers follow a shifting 'green belt' of vegetation that hosts highest grasshopper abundance (Trierweiler *et al.* 2013). The final wintering site of Montagu's Harriers is often located in the southern Sahel just at the southern edge of open savannah vegetation. Previously, we have shown that food abundance (grasshoppers) does decrease during their stay at the final wintering site, and more so in dry than wet years, and that GPS-tracked Montagu's Harriers responded to these deteriorating conditions by increasing their flight time (Schlaich *et al.* 2016). Individuals wintering in the driest conditions departed the latest in spring, suggesting that ecological conditions may carry-over to later annual cycle stages (Schlaich *et al.* 2016), even though there is no direct elevated mortality during the wintering period (Klaassen *et al.* 2014).

Here we provide a detailed description of wintering site use by individual Montagu's Harriers throughout the winter using a large tracking dataset of satellite as well as GPS-tracked individuals. We focus on the differences between sites where harriers stay after arrival from autumn migration (first sites), sites that they use before spring migration departure (last sites), and sites they use in-between (intermediate sites). We describe selection of sites (habitat composition and preferences) as well as site use (home range size and activity measures) in relation to environmental conditions. Furthermore, we investigate site fidelity and within-individual differences in timing and site use between years in relation to environmental conditions. This study elaborates on earlier work on wintering ecology (Trierweiler *et al.* 2013; Schlaich *et al.* 2016) through more detailed analyses of habitat selection and site use, including many individual harriers that were tracked in several consecutive years. This leads to the first steps in answering Moreau's question: 'The great problem is to know the extent to which an individual's movements in Africa, before settling into identically the same wintering site each year, are replicated during the lifetime of the migrant.' (Moreau 1972, page 266).

Materials and methods

All data selection procedures and analyses were performed in R 3.5.1 (R Core Team 2018). The R-packages and R-functions used are stated in the respective sections below.

Satellite-tracking data

We tracked 60 adult European Montagu's Harriers (24 males and 36 females) using solar-powered satellite transmitters (PTT-100 series, Microwave Telemetry Inc., Columbia, MD, USA) between 2005 and 2018. Birds were captured in breeding areas in Germany (n = 15), the Netherlands (n = 13), the United Kingdom (n = 12), Belarus (n = 8), Denmark (n = 8), and Poland (n = 4). Of those, 49 individuals (23 males and 26 females) produced tracks including wintering movements. Due to birds being tracked in consecutive years, a total of 106 wintering tracks (year*individual combinations) was accumulated. After removal of incomplete tracks (start or end missing, gaps), the final satellite-tracking dataset comprised of 78 tracks of 38 individuals (16 males and 22 females).

Satellite-transmitters were programmed either to a longer duty cycle of 10:48 h on:off (9.5 g and part of 12 g tags) or a shorter duty cycle of 6:16 h on:off (12 g tags) to recharge their batteries. Data were received via the ARGOS system (CLS, Toulouse, France). Raw data was filtered using R-function *sdafilter* from package *argosfilter* version 0.63 (Freitas 2012). Filtered data was checked visually and remaining outliers were removed.

GPS-tracking data

We tracked 65 adult European Montagu's Harriers (45 males and 20 females) using UvA-BiTS GPS trackers (Bouten *et al.* 2013; www.uva-bits.nl) between 2009 and 2018. Birds were captured in breeding areas in the Netherlands (n = 39), France (n = 12), and Denmark (n = 9), plus five at a wintering site in Senegal (Khelcom). Of those, 39 individuals (28 males and 11 females) returned to the study areas and tracks including wintering movements could be downloaded via the remote UvA-BiTS antenna system. A Danish male that oversummered in Africa (Sørensen *et al.* 2017) was removed from the dataset. Due to birds being tracked in consecutive years, a total of 63 wintering tracks (year*individual combinations) was accumulated. After removal of incomplete tracks (start or end missing, gaps), the final GPS-tracking dataset comprised of 51 tracks of 34 individuals (24 males and 10 females).

GPS trackers were programmed to collect GPS positions at an interval of 5 min (n = 15 tracks), 10 min (10), 15 min (20), or 30 min (6) during the day and at maximum once per hour during the night. Intervals differed because memory storage increased with newer trackers. Positions with instantaneous speeds or trajectory speeds higher than 25 m s^{-1} were removed from the dataset. In addition, data were checked for outliers visually.

Descriptive characteristics

Each point, in case of satellite-tracking data, or each day, for GPS-tracking data, was assigned an annotation (*wintering site* – stationary at a site, *trip* – explorative movement outside a site that could last one or several days but returned to the same site, or *switchover* – movement between consecutive wintering sites). For examples see Fig. S1. A stay at a wintering site was defined as lasting at least three days. Within a site, several night roosts could be used, but distance between consecutive roosts at a site are generally small (Fig. S1D,E). Consecutive wintering sites were defined as being at least 10 km apart with no overlapping tracks (cf. Fig. S1B). These annotations were done manually, since automated annotation using a threshold of distance between consecutive roosts did not define all wintering sites correctly. This was due to birds with large home ranges occasionally having inter-roost distances of more than 10 km. A geographical wintering site could be revisited during the same winter. For each site, we calculated a centroid using mean latitude and longitude of all positions at this site. Sites were grouped into three categories: first (first wintering site used after arrival from autumn migration), last (last wintering site used before departure on spring migration), and intermediate (all sites in-between, which could be more than one depending on how many sites an individual had used). In case only a single site was used, this was classified as last site.

Distance between consecutive sites was calculated using R-function *distMeeus* from package *geosphere* version 1.5-7 (Hijmans 2017). If switchover distance changed with date, thus during the course of the winter, (e.g. shorter distances between consecutive sites earlier in the winter) was modelled using a Linear Mixed-Effects Models (LMM) with *track* as random effect by means of R-function *lme* from package *nlme* version 3.1-137 (Pinheiro *et al.*

2018). Direction between sites was calculated using R-function *bearing* from package *geosphere*. Change of switchover direction during the course of the winter was modelled using an LMM with *track* as random effect. The difference in direction of switchovers during the first and second half of the winter was compared using a Pearson's Chi-squared test.

Arrival and departure date at the wintering grounds were defined as the first and last day at a stationary wintering site and retrieved from the annotated dataset. Differences in mean arrival and departure date between the sexes were investigated using an LMM with *track* as random effect. The length of stay at a site was the number of days spent at that site during a visit. The difference in length of stay between first and last sites was tested using a Pearson's Chi-squared test. The difference in length of stay at last sites compared to preceding sites was investigated using an LMM with *track* as random effect and the R-function *testInteractions* from package *phia* version 0.2-1 (De Rosario-Martinez 2015).

Habitat selection at wintering sites

We used the GlobCover 2009 V2.3 land use map (ESA GlobCover 2009 Project: http://due.esrin.esa.int/page_globcover.php) with a 300 m resolution to determine habitat selection of Montagu's Harriers for their wintering sites. The whole wintering zone of our tracked birds was defined as the 100% MCP (maximum convex polygon) around all wintering sites (except for one site that laid much out of range at the southern coast of Ghana, thus n = 449, Fig. S2). Sixteen of the 23 GlobCover land use categories occurred in the available zone (Fig. S3, Table S1), with only seven categories covering more than 5% of the surface area. Habitat types ranged from bare and sparsely vegetated to grassland and shrubland savannahs and mosaic or agriculture dominated habitats. These subsequent habitat types were spatially correlated and form more or less a gradient from north to south with increasing vegetation cover and agricultural productivity. Habitat types that are close to each other substitute each other whereas habitat types at the ends of the gradient exclude each other (Fig. S4). The habitat composition at Montagu's Harriers' wintering sites was determined by extracting habitat information from all GlobCover map cells within a radius of 3.53 km around each site centroid. Each such circle consisted of about 430 pixels of 300 x 300 m (ca. 39 km^2) which is similar to the average wintering home range size (median = 35 km^2, n = 193 sites; see Results). To illustrate individual variation in habitat use across sites, we ranked sites according to a habitat score. Habitat types increase in productivity with decreasing GlobCover values. For graphical purposes, we weighed the habitat types used by harriers with a value from 13 to one (see Table S1) and multiplied one-hundredth of the used percentage with the respective weighing factor. We then ordered the sites according to the sum of score values of all habitats (cf. Fig. 2.3B). The habitat score is a rank, but we realize that differences between the categories are not the same (difference habitat 1 to 2 is not the same as difference habitat 11 to 12). Nevertheless, high habitat scores indicate higher percentages of agricultural habitats which fits the geographical distribution of those (Fig. S5). To determine which habitat types were dominant at each site, we combined similar categories into three main habitat groups: agricultural, natural, and bare (see Table S1). Colours in graphs were chosen to show affiliation of habitats to the main groups: blues for bare and sparsely vegetated zones, greens for natural habitat types and reddish colours for agricultural habitats. A site was considered being dominated by one of these groups if the sum of all habitat types in one of the groups covered more than 50% of the surface area. If none of them did, the site was categorized into a forth group called "mixed". Frequencies were compared using Pearson's Chi-squared tests. Repeatability of habitat selection within individuals at successive sites was tested for using R-function *rpt* from package *rptR* version 0.9.21 (Stoffel *et al.* 2017).

Second order habitat selection (selection of home ranges (sites) within the study area) was analysed using compositional analysis (Aebischer *et al.* 1993) with the R-function *compana* from package *adehabitatHS* (Calenge 2006) for all wintering sites and for the three subsets of sites (first, intermediate, last) separately. The habitat composition at harrier sites was compared to the habitat composition at random sites. For this, 4500 (ten times the number of harrier wintering sites) random points were created within the maximum and minimum latitude and longitude of harrier sites using R-function *runifpoint* from package *spatstat* version 1.56-0 (Baddeley *et al.* 2015). As for the harrier wintering sites, habitat information from all GlobCover map cells within a radius of 3.53 km around each random point was extracted. Like this, we gained habitat information for comparable random sites. Subsets of random sites within the respective zone, defined as the 100% MCP of all sites or of one of the subsets of sites (MCP-all see red polygon Fig. S2, MCP-first, MCP-int. and MCP-last see Fig. 2.4A) were made (whole zone n = 3295, first n = 1585, intermediate n = 2408, last n = 2490 random sites) and habitat at those sites was considered as available habitat and compared to the used habitats by harriers. Habitat categories that occurred less than 1% in the available habitat were excluded and finally, nine habitat categories remained in the compositional analyses.

To investigate habitat diversity we compared Shannon's diversity indexes calculated using R-function *diversity* from package *vegan* version 2.5-2 (Oksanen *et al.* 2018) at the random sites to those of the wintering sites of our harriers. Frequency distributions of indexes were compared using t-tests.

In addition to habitat types, we used vegetation greenness at wintering and random sites as another environmental variable. It has been shown previously that vegetation greenness can be used as proxy for food availability (grasshoppers being the main prey in the winter diet of Montagu's Harriers (Szép & Moller 2005; Trierweiler & Koks 2009; Trierweiler *et al.* 2013; Schlaich *et al.* 2016). Therefore, we used NASA's MODerate resolution Imaging Spectroradiometer (MODIS) Normalized Difference Vegetation Index (NDVI) remotely sensed data (product MOD13Q1: data provided every 16 days at 250 m spatial resolution) downloaded from The Land Processes Distributed Active Archive Center (LP DAAC – https://lpdaac.usgs.gov) using R-package *MODISTools* (Tuck *et al.* 2014). Around each harrier wintering site centroid, 25 × 25 = 625 pixels of 250 × 250 m (~39 km^2, average wintering home range) were downloaded for the winters 2006/2007 till 2017/2018. The average of the 625 pixels was calculated for each 16-day period after removal of fill values (–3000) and then multiplied by the scaling factor of 0.0001 to get NDVI values between –0.2 and 1. The same was done for 750 of the random points within the MCP-all. Of those, 346 lay within MCP-first, 550 within MCP-int, and 567 within MCP-last. To compare vegetation greenness between harrier sites and random sites, we used the closest NDVI values to three dates: the peak of harrier presence at first, intermediate and last sites (derived from Fig. 2.1B).

These were NDVI measures on 30 September, 1 November, and 6 March, respectively (in the leap years 2008, 2012, and 2016 these dates were 29 September, 31 October, and 5 March, respectively). We selected the values on those dates of all 12 winters for harrier sites (n = 5400 NDVI measures, first: 1500, intermediate: 2352, last: 1548) as well as random sites (n = 17,556, first: 4152, intermediate: 6600, last: 6804) and compared the frequency distributions using t-tests. To determine how dry or wet a year was in general, we calculated a *yearNDVI* value for each year. This was done by using the mean NDVI values of the three dates for the 750 random points and calculating a median NDVI over these 750 values per year.

Home range size and activity measures

For this part, we only used data of the GPS-tracked Montagu's Harriers since these were much more precise and much denser (on average 92 positions per day compared to on average four positions per day for satellite tracks). Days with fewer than 75% of expected positions (<108 for 5 min, <54 for 10 min, <36 for 15 min, <27 for 20 min, and <18 for 30 min interval tracks) were removed from this dataset. Two tracks had too many days with few data and were removed, thus 49 tracks remained. Switchover days as well as trip days were removed from the dataset.

Daily home ranges were calculated as 90% kernel density estimation using R-function *rhrKDE* from package *rhr* version 1.2.909 (Signer & Balkenhol 2015) with bandwidth parameter *h* determined by reference bandwidth estimation using R-function *rhrHref*. Surface area of daily home ranges was retrieved using R-function *rhrArea*. For the calculation of daily activity measures, only positions during daylight were used (daylight being defined as being between nautical dawn and nautical dusk). Time spent flying and distance covered were calculated for each day. We determined for each GPS position if the bird was sitting or flying using instantaneous speed and a threshold of 1.2 m s^{-1} (local minimum of a two-peaked frequency distribution of instantaneous speeds). The percentage of positions in flight was corrected by day length to determine the number of hours spent flying per day. Cumulative daily distance was calculated as the sum of distances between positions during a day. Distance between consecutive positions was calculated using R-function *distMeeus* form package *geosphere*. Temporal patterns in daily home range size, hours flying per day, and daily distance were analysed using a Linear Mixed Effects Model (LMM) with *site category* as fixed effect and *year* as well as *site ID* nested in *individual* as random effects by means of R-function *lmer* from package *lme4* version 1.1-17 (Bates *et al.* 2015) in combination with package *lmerTest* version 3.0-1 (Kuznetsova *et al.* 2017) and R-function *testInteractions*.

We calculated the total size of wintering site home ranges (using all positions at a wintering site) using the Biased Random Bridge Movement Model (BRBMM, Benhamou 2011) which is a movement-based kernel density estimation to estimate the Utilization Distribution (UD) of an animal with serial autocorrelation of the relocations using R-function *BRB* from package *adehabitatHR* version 0.4.15 (Calenge 2006). Tmax was set to 15 times the GPS interval since home range size became stable from this value onwards for the different intervals (data not shown). We used the surface area of the 90% contour of the UD retrieved using R-function *getverticeshr* from package *adehabitatHR* to determine total site home range size. Differences in total home range size between first, intermediate and last sites were analysed using an LMM with *site category* as fixed effect and *year* as well as *site ID* nested in *individual* and *number of days* as random effects and R-function *testInteractions*. Spatial patterns in total home range size were modelled using a Linear Model (LM) with *latitude* and *longitude* as fixed effects. The effect of environmental variables on total home range size was investigated using each an LMM with *NDVI* or *habitat score* as fixed effects as well as *site ID* nested in *individual* as random effects. If home range size differed between dry and wet years, was also analysed in an LMM with *yearNDVI* as fixed effect as well as *site ID* nested in *individual* as random effects.

Site fidelity

The dataset of repeated tracks comprised of 33 individuals of which 19 were tracked in two years, six in three years, six in four years, and two in five years. In total, these birds have used 164 different geographical sites which have been visited in one or in several years by the same individual. Each geographical site was given a *site-ID* and classified into one of the three site categories (first/intermediate/last) by defining that a site that was once used as first site was named “first” irrespective if it had been used as an intermediate site in any other year. Whenever a site had been used as a last site it was named “last” even though it had been used as intermediate site in another year. Sites that were only used as intermediate sites but never as first or last, were called “intermediate”. In two cases, a site was used as first site in one and as last site in a second year and these were classified as “last”.

Overall site fidelity was calculated as the percentage of sites re-used by an individual between two years. For this, we took the sites visited by an individual in year 1 and counted how many of those it re-used in year 2. If all sites were used in both years, the individual showed 100% site-faithfulness. If for example only one out of two of the sites were re-visited in year 2, it showed 50% site-faithfulness, irrespective of new sites used in year 2. We did several two-year comparisons for birds with more than two years of tracking, that means we compared year 1 to year 2, year 2 to year 3, and so on. To determine site fidelity for first, intermediate and last sites separately, we then subset the dataset to each of the three categories and checked if a site used in year 1 was also used in year 2.

To investigate in more detail how often a site was re-used in relation to site category and duration of stay, we created a new dataset using only birds that were tracked in at least three years (n = 14). In case a bird was tracked in more than three years, we used its first three years for this analysis. With this balanced dataset we could determine if a site was used in all three years or only in one or two of the three years (*re-use category* 1, 2 or 3). Differences in duration of stay between sites were tested for using a Linear Model *with re-use category* and *site category* as fixed effects.

Within-individual differences in relation to environmental conditions

The variation within an individual between years and between individuals was investigated for several variables using within-subject centring in mixed models as described in van de Pol and Wright (2009). This procedure allows to separate within-individual effects from between-individual effects by using the relative values (observation(ind,year) – mean observation (ind)) as well as the individual’s mean as predictor variables in a mixed model with individual as random effect. For example, to explain the number of sites that an individual used in a winter in response to the environment (*yearNDVI*), the model looked like this:

lme(number of sites ~ relative *yearNDVI* + mean individual *yearNDVI*, random = ~1|individual).

We used this procedure to investigate within- and between-individual effects of local NDVI on several response variables. For this, we used all sites that were at least used twice (n = 71) and calculated a mean NDVI value for the period that the bird had stayed at this site. These NDVI values thus are the mean of a different number of NDVI measurements (one every 16 days) depending on duration of stay. If no NDVI measurement lay exactly within the period that the bird used the site (short visit), we used the first NDVI measurement after the bird had left. For each site, a mean NDVI value was calculated over the years the site had been used, as well as the relative NDVI (difference of the NDVI at the site in that year minus the mean site NDVI).

Home range size and activity measures for GPS-tracked birds were available at 24 sites of 10 individuals used in two (n = 16), three (4), or four (4) years. Using one of the following response variables: site home range size, mean hours flying per day, mean daily distance, we investigated within- and between-individual effects by including *relative NDVI* and *mean site NDVI* as fixed effects and *siteID* nested in *individual* as random effect.

Timing of movements between sites was investigated for all birds, irrespective of tracking method. Within-individual differences in timing of movement between sites in relation to NDVI were tested in the same way. We used the departure date from first sites as well as the duration of stay at first sites (subset of 20 sites from 17 individuals), the duration of stay at intermediate sites (subset of 19 sites from 16 individuals), and the arrival date at last sites (subset of 32 sites from 30 individuals) as response variables. *Relative NDVI* and *mean site NDVI* were included as fixed effects and *siteID* nested in *individual* as random effect. All model output is given in Table 2.1.

Results

General description of strategy of itinerancy

European Montagu's Harriers used wintering sites between 5.9°N and 18.1°N and between 17.1°W and 17.6°E (129 complete tracks of 72 individuals (32 females and 40 males; GPS-trackers: 51 tracks of 34 individuals, satellite transmitters: 78 tracks of 38 individuals), 2006-2018; Fig. 2.1A). During a winter, these birds used on average 3.3 ± 1.1 (range 1–6) different geographical sites (Fig. 2.2). The average number of site visits was a bit higher (3.5 ± 1.3, range 1–8) because 14 individuals out of 74 (19.4%) revisited geographical sites during the same winter. In total, 23 sites were revisited, most of them only once (21 occurrences) and two of them twice. Revisits occurred in 13% of tracks (17 out of 129 tracks) where birds revisited a single site during a winter (11 tracks) or even revisited two sites (6 tracks). Three birds (two of them twice) returned to their first site as last site (cf. Fig. 2.2). Use of a single wintering site occurred only in 3% of tracks (4 out of 129), twice by an individual in two consecutive years, once by an individual tracked in a single year and once in

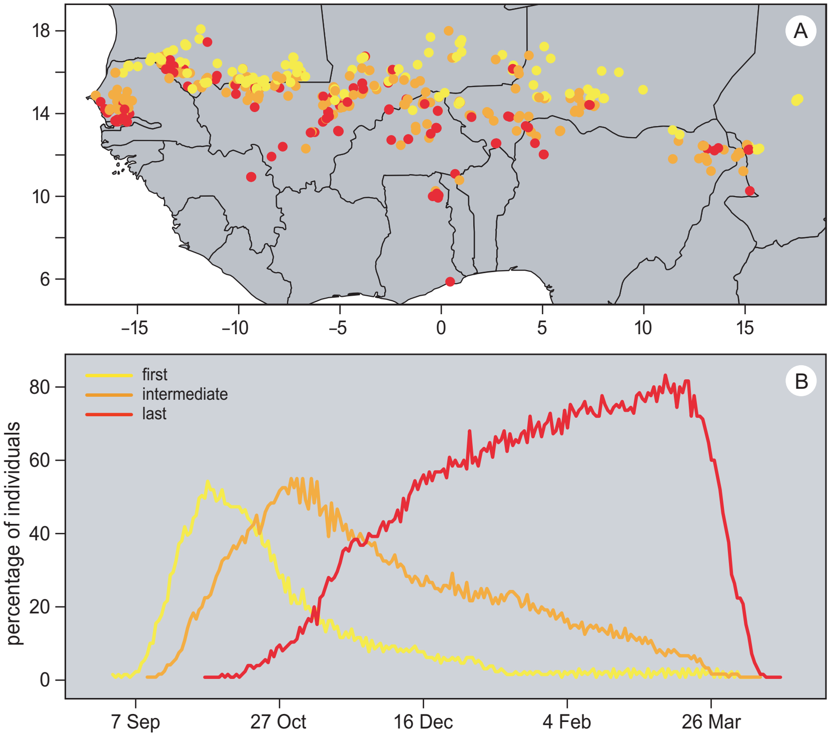

Figure 2.1. (**A**) Wintering sites of European GPS- and satellite-tracked Montagu's Harriers (n = 129 winters). (**B**) Percentage of individuals at first, intermediate and last sites during the wintering season.

an individual that had five sites in the next year. Consecutive sites were on average 229 ± 238 km (10–1434 km, median = 135 km, n = 321 site switchovers) apart. The travel distance between sites did not change with date during the course of the winter (LMM: $t = -1.255$, df = 195, $P = 0.211$). Mean direction between consecutive sites was 194° ± 73° (SbW, range 5–359°, n = 321 site switchovers). Direction changed with date over the season (LMM: $t = -5.213$, df = 195 $P < 0.001$). Switchovers in the first half of the winter (before 15 December) were on average directed SSW (207 ± 57°) and switchovers after 15 December SSE with a wider spread (158 ± 97°; significant difference in frequencies, Pearson's Chi-squared test: $\chi^2 = 86.6$, df = 15, $P < 0.001$). Mean arrival date at the wintering grounds was 23 September ± 9 days (range 30 August–19 October, n = 129) and did not differ between the sexes (LMM: $F = 1.96$, df = 127, $P = 0.164$). Departure was on average on 30 March ± 8 days (range 05 March-20 April, n = 129). Males departed on average 4.5 days earlier than females (LMM: $F = 10.57$, df = 127, $P < 0.01$). Winter had thus a total length of 188 ± 12 days (151–213 days, n = 129) of which 9 ± 7 days (0–37 days, n = 125) were switchover days on which birds moved between consecutive wintering sites. Site visits lasted on average 52 ± 47 days (3–196 days, n = 450 visits). Length of stay at the first site of a wintering season (29 ± 23 days, 3–105 days, median = 25 days, n = 125) was significantly shorter than at the last site (103 ± 49 days, 4–196 days, median = 113, n = 129; Pearson's Chi-squared test: χ^2 =

126.97, df = 5, $P < 0.001$; Fig. 2.1B). The length of stay at the last wintering site was significantly longer than at all preceding sites (LMM: $F = 58.86$, df = 314, $P < 0.001$).

Habitat composition at wintering sites

There was a great variation of habitat composition at harrier wintering sites (Fig. 2.3AB). Sites ranged from being composed mostly of bare and sparsely vegetated habitat types to nearly inclusively being located in agricultural habitats with all possible combinations on the gradient in-between (distribution of habitat types for all sites see Fig. 2.3B). Since no clearly separated groups could be distinguished, we summarized the results by grouping sites dominated by one of the main dominant habitat groups (Fig. 2.3C). Around 30% of sites were dominated by sparsely vegetated habitats at first sites, this decreased to about 10% at intermediate and last sites. Sites dominated by agricultural habitats increased significantly from 20% at first to nearly 50% at intermediate sites and remained that high at last sites. Sites dominated by natural habitat types were mostly found at first sites (46%), this decreased at intermediate and last sites to about 30%. Frequencies of dominant habitats differed significantly between the three subsets (Chi-squared test: $\chi^2 = 49.65$, df = 6, $P < 0.001$). The frequencies differed significantly between first and intermediate sites (Chi-squared test: $\chi^2 = 36.26$, df = 3, $P < 0.001$) as well as first and last sites (Chi-squared test: $\chi^2 = 39.53$, df = 3, $P < 0.001$), but not between intermediate and last sites (Chi-squared test: $\chi^2 = 1.19$, df = 3, $P = 0.755$). Repeatability of habitat selection within individuals at successive sites (within season) was high (repeatability estimate from LMM: R = 0.24, SE = 0.052, CI = [0.131, 0.331], $P < 0.001$) which might be due to regional differences in habitat composition (Fig. S4).

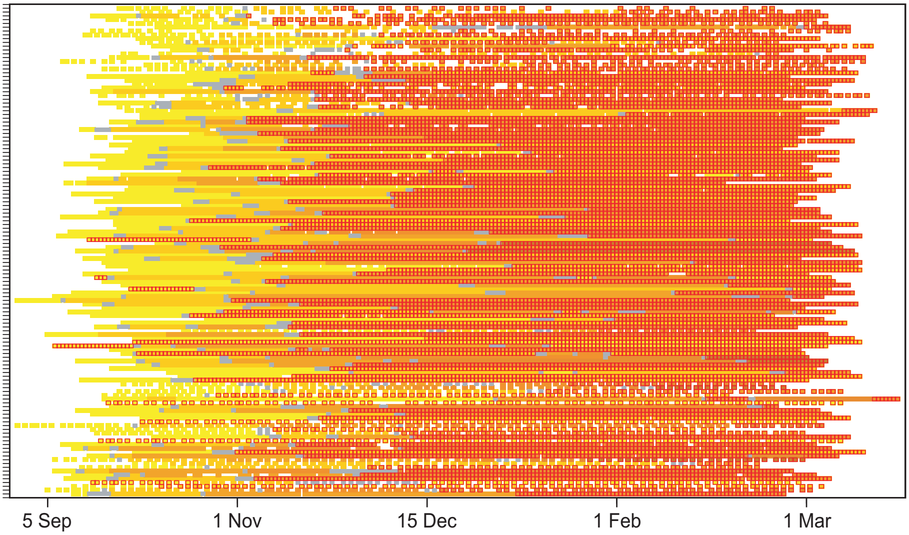

Figure 2.2. Site use pattern of European GPS- and satellite-tracked Montagu's Harriers (n = 129 winters). Each row resembles one winter. For y-axis labels see Table S2. Colours indicate different sites: first sites yellow, consecutive sites in darkening orange colours. Days at last sites are marked with a red rectangle. Travel days between consecutive sites are indicated in grey. Days with no available data are visible as white rectangles.

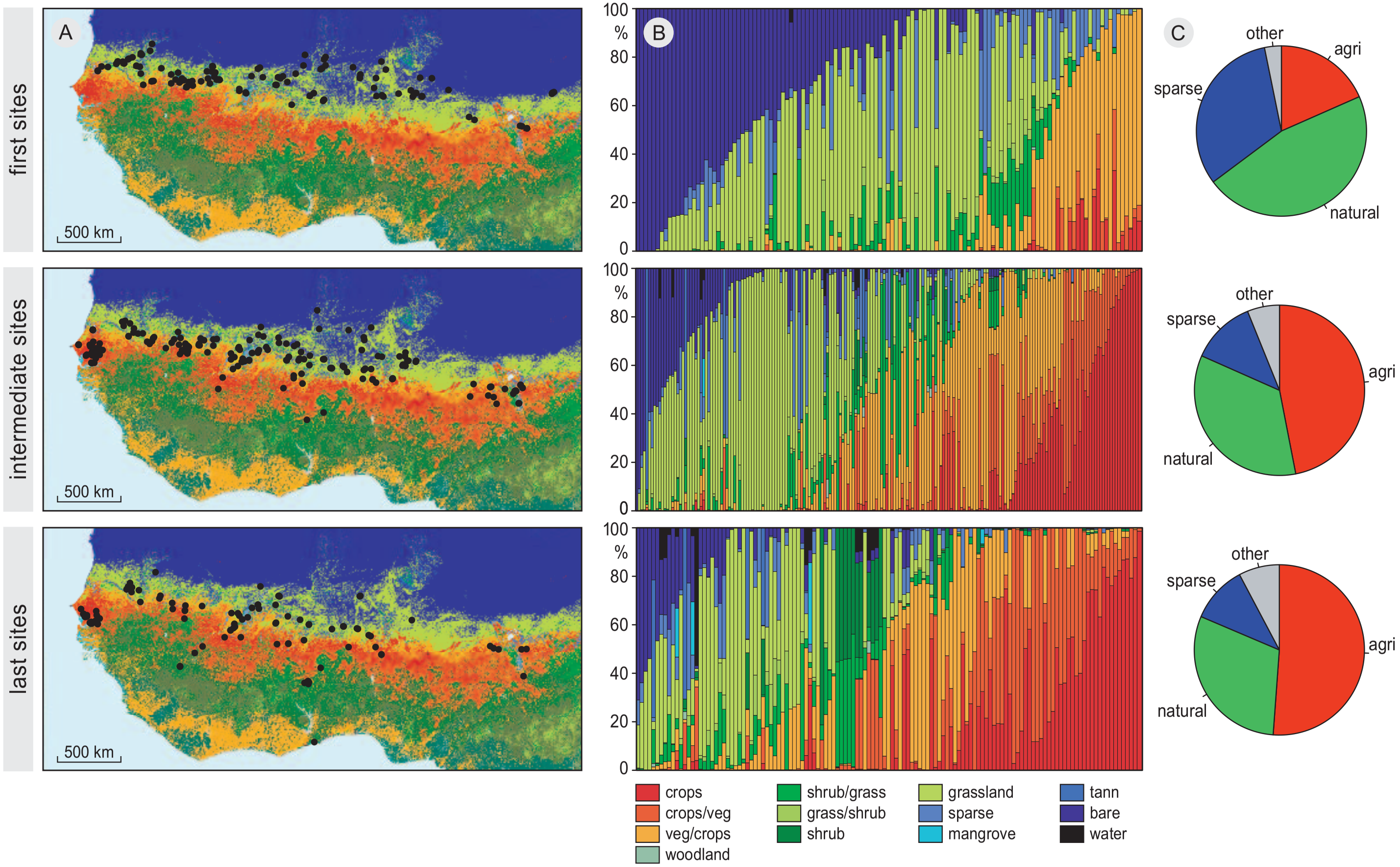

Figure 2.3. Habitat composition at wintering sites of GPS-tracked Montagu's Harriers for first (n = 57), intermediate (99) and last sites (59). (**A**) Location of wintering site centroids shown on GlobCover land use map. (**B**) Habitat use per site, each bar represents one site, ordered according to habitat score for graphical purposes. (**C**) Dominant habitats.

Habitat preferences of harriers

Overall, compared to random points within the MCP-all, Montagu's Harriers preferred at their wintering sites grassland, mosaic vegetation/cropland, mosaic shrubland/grassland and sparse vegetation over the five remaining habitat types. Bare areas, mosaic cropland/vegetation and cropland were less preferred. Woodland and shrubland were significantly avoided (Compositional analysis: $\lambda = 0.258$, $P = 0.01$; Fig. S6). At first sites, harriers significantly preferred grassland over sparse vegetation, bare areas, mosaic shrubland/grassland, and mosaic vegetation/cropland. Least preferred at first sites were woodland, cropland and mosaic cropland/vegetation. Shrubland was significantly avoided (Compositional analysis: $\lambda = 0.057$, $P = 0.01$; Fig. 2.4B). This changed at intermediate sites were harriers preferred mosaic vegetation/cropland and grassland as well as mosaic shrubland/grassland, sparse vegetation mosaic cropland/vegetation, cropland and bare areas. Woodland and shrubland were significantly avoided (Compositional analysis: $\lambda = 0.276$, $P = 0.01$; Fig. 2.4B). At last sites, the ranking order changed slightly. Mosaic vegetation/cropland and mosaic shrubland/grassland were again most preferred followed by mosaic cropland/vegetation, cropland, sparse vegetation and grassland. Bare areas, woodland and shrubland were least preferred (Compositional analysis: $\lambda = 0.166$, $P = 0.01$; Fig. 2.4B).

Overall, Montagu's Harriers selected wintering sites with significantly higher habitat diversity than available at randomly distributed sites (Fig. S7; n = 450 harrier wintering sites, n = 3295 random sites; t-test: $t = -6.188$, df = 565.19, $P < 0.001$). Habitat diversity was highest at last sites (mean 0.96, n = 129), followed by intermediate sites (0.82, n = 196), and first sites (0.81, n = 125; Fig. 2.4C). It differed significantly between first and last sites (t-test: $t = -2.794$, df = 248.68, $P < 0.01$) as well as between intermediate and last sites (t-test: $t = -2.777$, df = 303.32, $P < 0.01$) but not between first and intermediate sites (t-test: $t = -0.216$, df = 280.08, $P = 0.829$). Habitat diversity at first and last sites was significantly higher than at random sites within their respective MCPs (Fig. 2.4A,C; t-test: first: $t = 2.083$, df = 10046, $P = 0.037$; last: $t = -3.772$, df = 139.82, $P < 0.001$), but did not differ at intermediate sites (t-test: $t = -0.939$, df = 218.5, $P < 0.349$).

Montagu's Harriers selected wintering sites with slightly lower vegetation greenness (NDVI) than available at randomly distributed sites (Fig. S8; n = 5400 NDVI values at harrier wintering sites, mean 0.23; n = 17,556 NDVI values at random sites, mean 0.24; t-test: $t = -6.188$, df = 565.19, $P < 0.001$). Vegetation greenness was highest at intermediate sites (mean 0.26, n = 2352), followed by first sites (0.23, n = 1500), and last sites (0.19, n = 1548; Fig. 2.4D). It differed significantly between first and intermediate sites (t-test: $t = -9.333$, df = 3352, $P < 0.001$), first and last sites (t-test: $t = 14.375$, df = 2096.2, $P < 0.001$), as well as intermediate and last sites (t-test: $t = 28.971$, df = 3448.3, $P < 0.001$). Vegetation greenness at first sites was significantly higher than at random sites within the respective MCP (Fig. 2.4A,D; n = 4142 NDVI values at random sites within MCP-first, mean 0.20; t-test: $t = -10.106$, df = 2409.6, $P < 0.001$). On the contrary, harriers chose sites with significantly lower NDVI values at intermediate sites (n = 6600 NDVI values at random sites within MCP-int, mean 0.29; t-test: $t = 9.591$, df = 5205.2, $P < 0.001$) and last sites (n = 6804 NDVI values at random sites within MCP-last, mean 0.21; t-test: $t = 11.554$, df = 2965.4, $P < 0.001$).

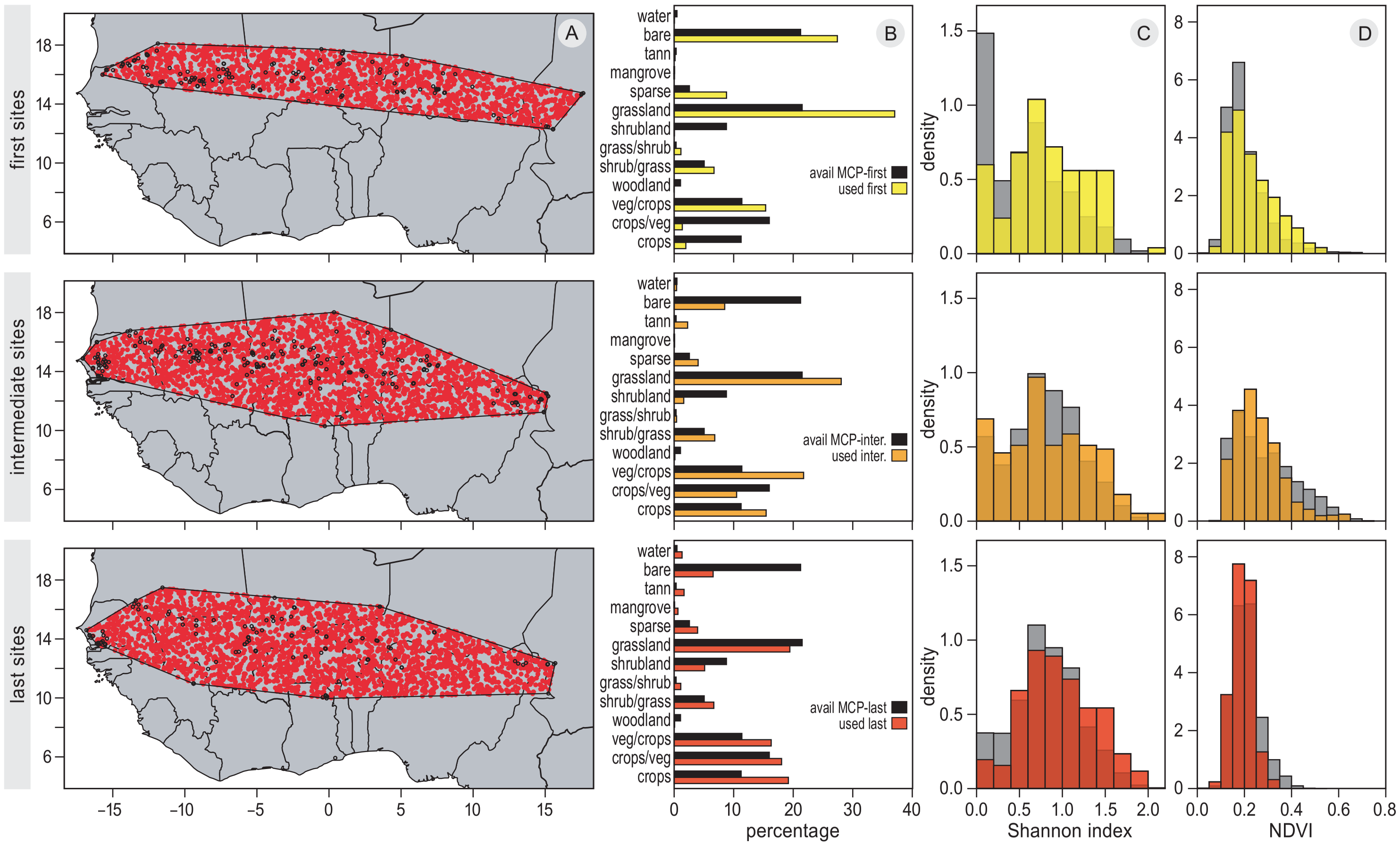

Figure 2.4. (**A**) Montagu's Harrier wintering sites (black points) and 100% MCP for first, intermediate and last sites. (**B**) Habitat used at harrier sites compared to wintering range MCPs. (**C**) Habitat diversity calculated as Shannon's diversity index for harrier wintering sites compared to random sites (grey bars). (**D**) NDVI (Normalized Difference Vegetation Index) at harrier wintering sites compared to random sites (grey bars).

Home range size and activity measures

Daily home range size was smallest at intermediate sites (mean = 25.7 km^2), slightly larger at first sites (28.6 km^2, LMM: χ^2 = 1.518, *P* = 0.218) and significantly larger than both at last sites (51.22 km^2, first-last: χ^2 = 13.618, *P* < 0.001, intermediate-last: χ^2 = 30.471, *P* < 0.001; Fig. 2.5B). Montagu's Harriers flew fewest at first sites (mean = 3.86 hours per day), a bit more at intermediate sites (3.93, LMM: χ^2 = 18.749, *P* < 0.001) and much more at last sites (4.71, first-last: χ^2 = 6.017, *P* = 0.014, intermediate-last: χ^2 = 52.929, *P* < 0.001; Fig. 2.5A). Daily distance covered was also shortest at first sites (mean = 25.1 km), increased at intermediate sites (25.8 km, LMM: χ^2 = 8.812, *P* < 0.01) and was longest at last sites (33.1 km, first-last: χ^2 = 0.459, *P* = 0.498, intermediate-last: χ^2 = 5.168, *P* = 0.046; Fig. 2.5C).

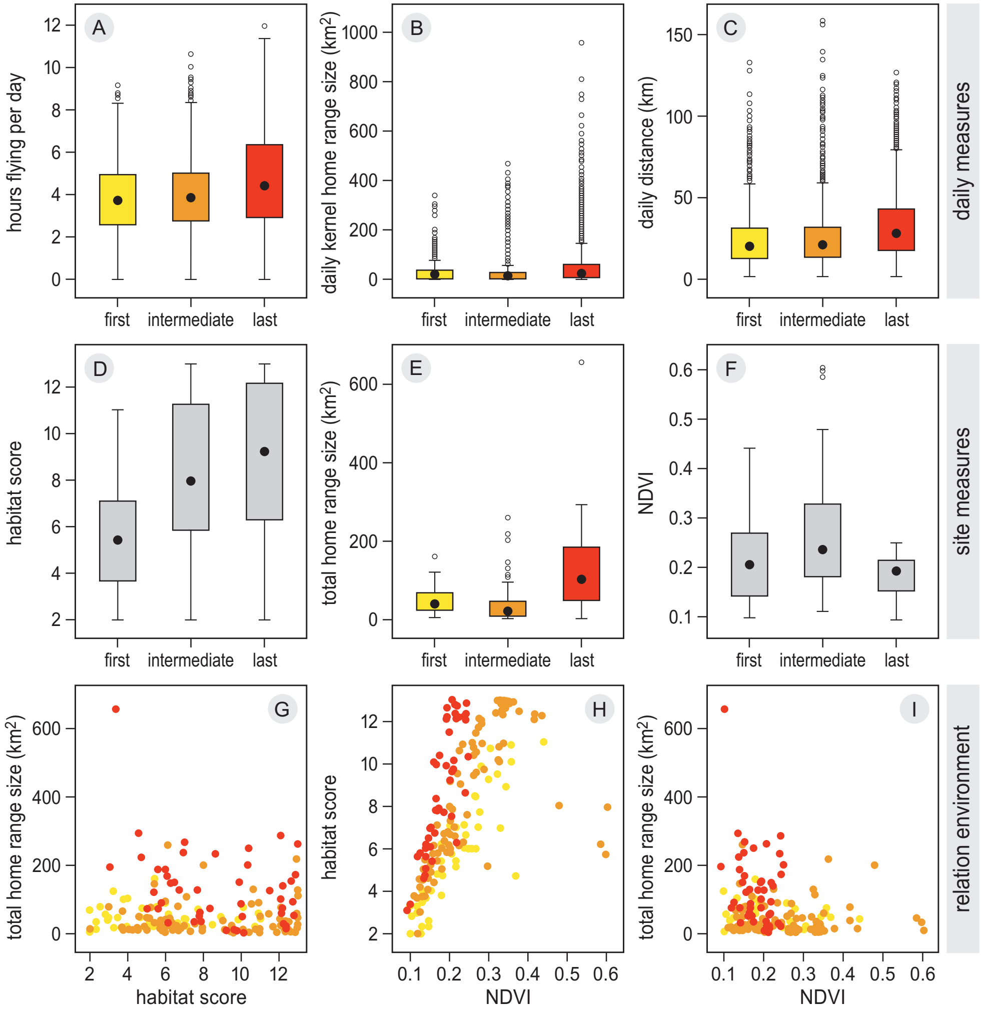

Figure 2.5. Daily activity measures of GPS-tracked Montagu's Harriers (**A-C**), environmental variables (**D**,**F**) and total site home ranges (**E**). Relation between total home range and environmental variables (**G**,**I**), as well as between environmental variables (**H**).

The median total site home range size of Montagu's Harriers' wintering sites was 35 km^2 (mean = 63 km^2, range 3 – 656 km^2, n = 193 sites; Fig. S9). Total site home range size was smallest for intermediate sites (median = 21 km^2), not significantly bigger for first sites (39.7 km^2, LMM: $\chi^2 = 0.851$, $P = 0.356$), but much bigger than both for last sites (101 km^2, first-last: $\chi^2 = 43.194$, $P < 0.001$, intermediate-last: $\chi^2 = 70.003$, $P < 0.001$; Fig. 2.5E). Total site home range size did not differ with latitude (LM: $t = -0.048$, $P = 0.962$) or longitude ($t = 0.421$, $P = 0.674$). However, total site home range size did decrease significantly with greenness values (LMM: $t = -3.83$, df = 187.54, $P < 0.001$; Fig. 2.5F,I) but did not differ with habitat score ($t = -0.72$, df = 138.63, $P = 0.472$; Fig. 2.5D,G). NDVI and habitat score were correlated (Fig. 2.5H) with higher NDVI values coinciding with higher habitat scores, thus more covered and more agricultural habitats. Total site home range size did not differ with *yearNDVI* (LMM: $t = 0.93$, df = 2.23, $P = 0.44$; Fig. 2.6).

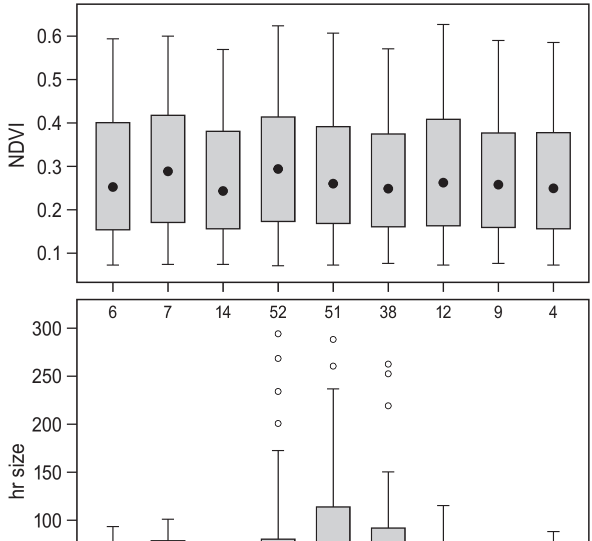

Figure 2.6. YearNDVI (top) and home range size (bottom) for the years GPS-tracked Montagu's Harriers were followed. The number of site home ranges per year is given above the boxplots.

Site fidelity

Montagu's Harriers tracked in two consecutive years, used three-quarter of their wintering sites visited in the first year again in the next year (median = 75%, 1st Qu. = 50%, 3rd Qu. = 100%, n = 57 two-year comparisons). First sites were re-used in the next year in 60% of cases (n = 60 two-year comparisons), intermediate sites in 50% (n = 52), and last sites in 91% of cases (n = 64).

When investigating the use of geographical sites in more detail using a dataset of birds that were tracked in three years, we saw that first and intermediate sites were used once, twice or thrice. Last sites however, were mostly used in all three years and only occasionally in a single year (Fig. 2.7A). The duration of stay at a site was longer for sites used in several years and harriers stayed longer at last sites than at first or intermediate sites (Fig. 2.7B).

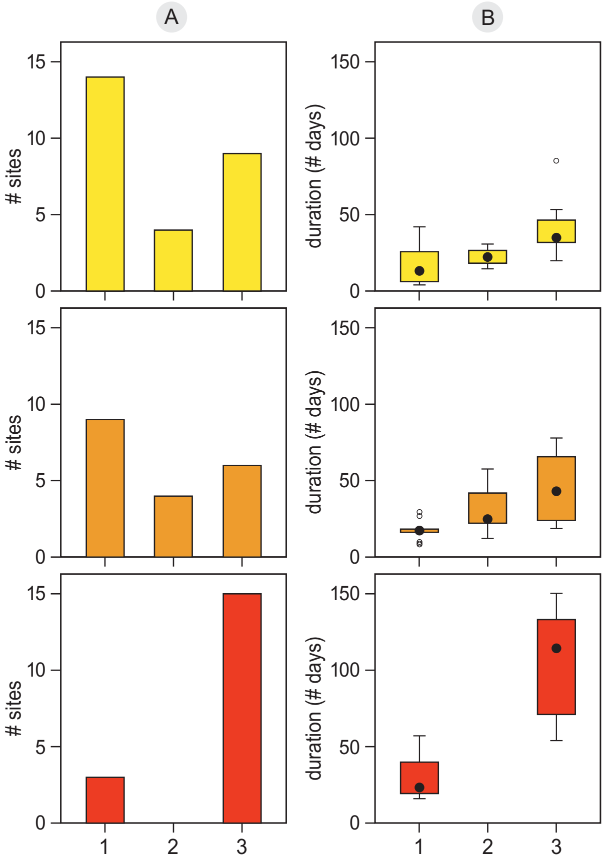

Figure 2.7. Re-use of geographical sites by individuals tracked in three consecutive years. (**A**) Sites re-used once, twice or thrice during these three years for first (top), intermediate (middle) and last sites (bottom). (**B**) Length of stay at these sites according to re-use category and site category. Both significantly influenced length of stay (Linear Model: re-use category F = 39.5, df = 2, $P < 0.001$; site category F = 21.97, df = 2, $P < 0.001$).

Within-individual differences in relation to environmental conditions

Montagu's Harriers tracked in several years sometimes added or skipped one or more sites compared to the previous year. Whether it was a drier or wetter year (*yearNDVI*) did neither explain within-individual nor between-individual variation (Table 2.1a).

GPS-tracked harriers' home range size at the same geographical site compared between years did not depend on local NDVI at the moment of presence. However, we found significant between-individual effects with individuals wintering in dryer areas having larger home ranges (Table 2.1b, Fig. 2.8A). The same was true for the time harriers spent flying, no within-individual effects but significant between-individual effects with individuals wintering in dryer areas flying more (Table 2.1c, Fig. 2.8B). Only the mean daily distance

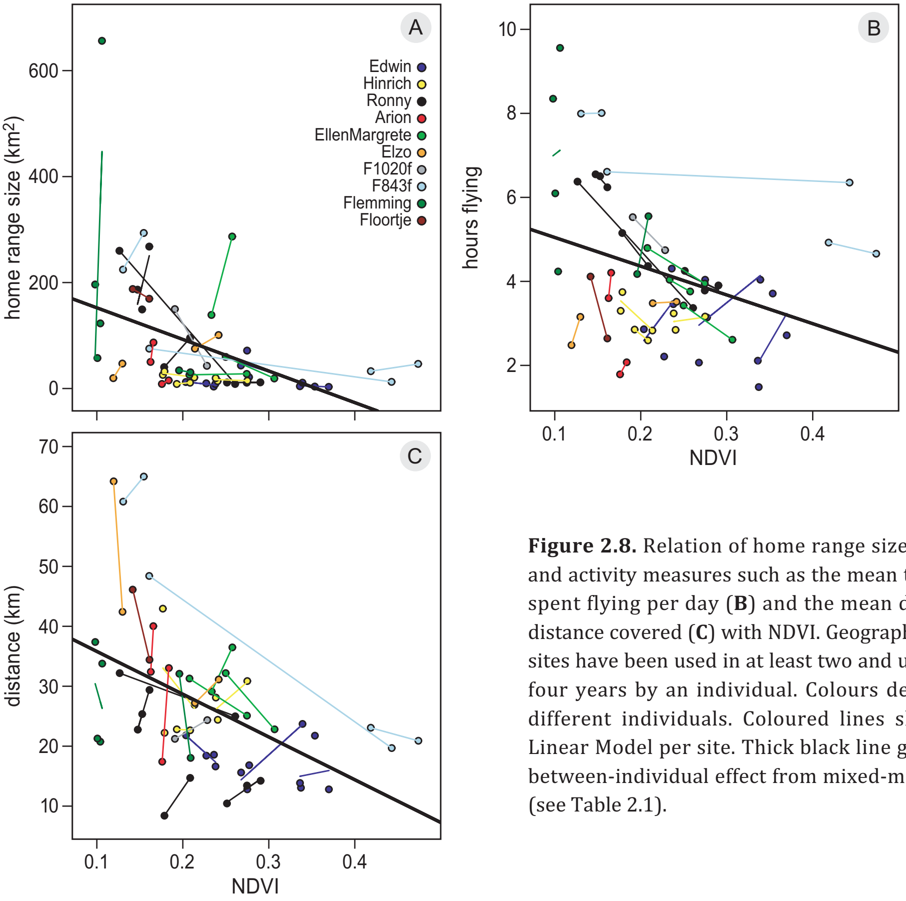

Figure 2.8. Relation of home range size (**A**) and activity measures such as the mean time spent flying per day (**B**) and the mean daily distance covered (**C**) with NDVI. Geographical sites have been used in at least two and up to four years by an individual. Colours depict different individuals. Coloured lines show Linear Model per site. Thick black line gives between-individual effect from mixed-model (see Table 2.1).

Table 2.1. Model output for several variables using within-subject centring in mixed models as described in van de Pol & Wright (2009).

	Within–individual effect NDVI					Between–individual effect NDVI				
	Estimate	SE	df	*t*–value	*P*–value	Estimate	SE	df	*t*–value	*P*–value
(a) Number of sites	−4.57	8.37	53	−0.55	0.59	−39.18	29.8	28	−1.31	0.2
(b) Home range size	−369.76	351.41	35	−1.05	0.3	−634.86	198.37	13	−3.2	**0.007**
(c) Hours flying	−3.81	3.83	35	−0.99	0.33	−9.88	2.42	13	−4.09	0.001
(d) Daily distance	−70.61	25.62	35	−2.76	**0.009**	−104.55	20.34	13	−5.14	<0.001
(e) Departure first	123.86	47.37	35	2.61	**0.013**	56.26	112.08	2	0.5	0.67
(f) Duration first	133.06	47.7	35	2.79	**0.009**	84.42	84.52	2	1	0.42
(g) Duration intermed.	27.23	96.8	26	0.28	0.78	57.19	101.01	3	0.57	0.61
(h) Arrival last	−450.39	250.56	58	−1.8	0.07	−215.66	115.79	1	−1.86	0.31

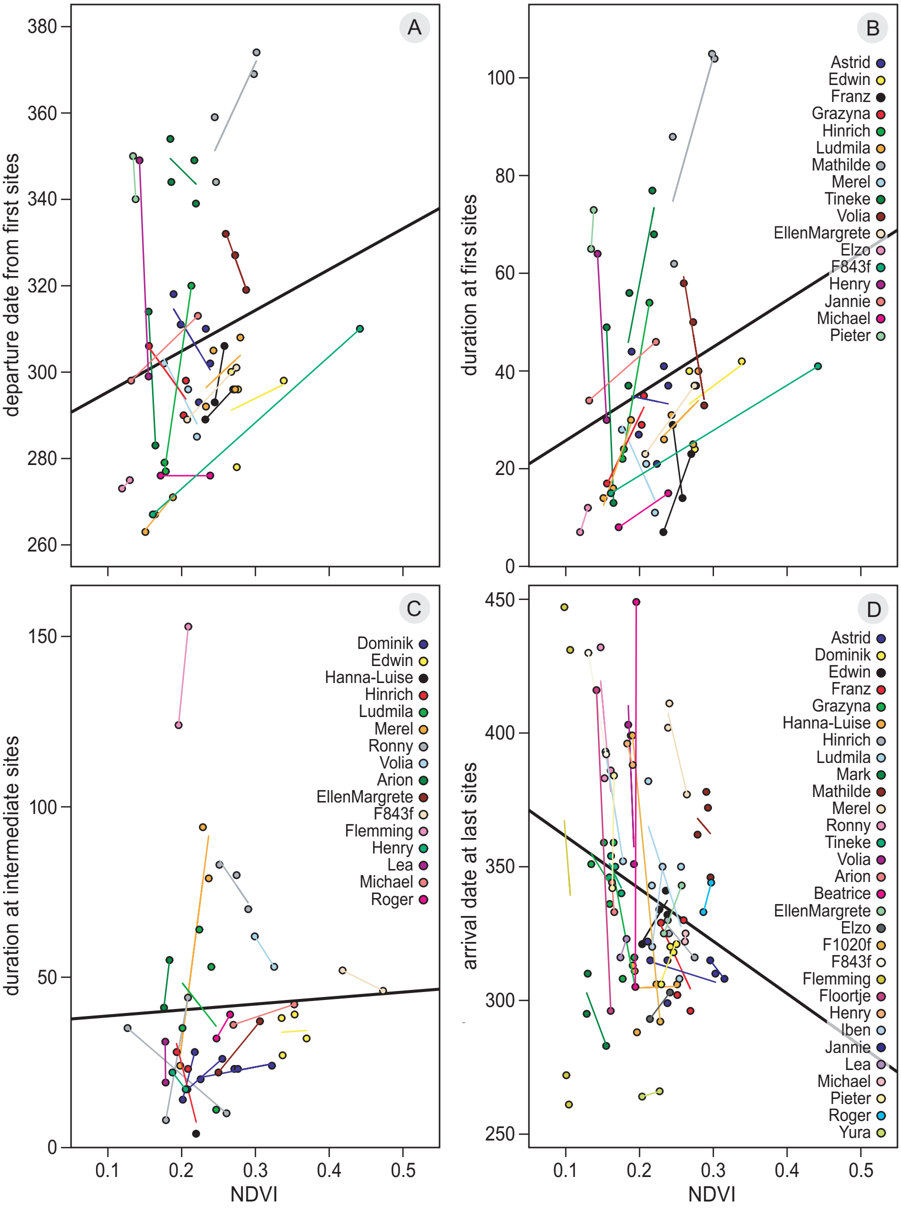

Figure 2.9. Relation of timing of movements between wintering sites with NDVI. Geographical sites have been used in at least two and up to five years by an individual. Colours depict different individuals. Coloured lines show Linear Model per site. Thick black line gives between-individual effect from mixed-model (see Table 2.1).

flown at a site revealed a significant within-individual effect with birds flying more kilometres at the same site in a dryer year, as well as a between- individual effect with individuals wintering in dryer areas flying more kilometres (Table 2.1d, Fig. 2.8C).

Within-individual differences in timing of movements between sites could mainly be explained by local NDVI at the moment of presence. Harriers departed on average significantly earlier from a first site in a dryer year than from the same site in a greener year (Table 2.1e, Fig. 2.9A) and consequently stayed significantly longer at a first site when it was greener (Table 2.1f, Fig. 2.9B). The duration of stay at intermediate sites was not dependent on NDVI (Table 2.1g, Fig. 2.9C). Arrival date at last sites had however a strong tendency to be earlier in greener years compared to the arrival date at the same site in a dryer year (Table 2.1h, Fig. 2.9D). There were no between-individual effects in timing of movement (Table 2.1e-h) which means that individuals have no fixed behavioural response but show plastic behaviour by reacting to local environmental conditions.

Discussion

By using a large dataset of satellite and GPS-tracked harriers, we confirmed that Montagu's Harriers pursue an itinerant wintering strategy, having multiple wintering sites. Harriers started wintering in the northern Sahel and moved southwards via intermediate sites to their last wintering site where they stayed longest and had the largest home ranges, especially individuals in drier conditions. They selected mosaic habitats with a large component of agricultural use, and preferred sites with higher habitat diversity. Individuals tracked over multiple years did re-use sites often, and were especially site-faithful to last wintering sites. We found evidence that timing of movements was flexibly adjusted to within-individual variation in environmental conditions: at the same site, individuals flew larger distances per day when conditions were drier, and leaving the first site earlier when encountered conditions in a year were drier. Although we found no such pattern for intermediate sites, we found within-individual effects in arrival at the last site, being earlier when conditions were supposedly beneficial (more green vegetation). Interestingly, many of these effects were only observed on a within-individual level, illuminating that variation between individuals in wintering conditions may obscure individual flexible responses to environmental conditions. Our data show clearly that itinerancy in Montagu's Harriers is a flexible adjustment to between-year variation in environmental conditions encountered at their different local wintering sites.

Itinerancy

Using a very large tracking dataset, our results deepen previous work showing that Montagu's Harriers wintering in West Africa are itinerant during winter (Trierweiler *et al.* 2013). With increasing information on wintering strategies thanks to tracking data, it appears that most species show itinerancy. Even species Moreau (1972) and Newton (2008) suspected to perform nomadic movements have been shown to be itinerant, occupying several distinct wintering residency sites, like White Stork *Ciconia ciconia* (Berthold *et al.* 2001, 2002, 2004), Lesser Spotted Eagle *Clanga pomarina* (Meyburg *et al.* 2015), and Lesser

Kestrel *Falco naumanni* (Rodríguez *et al.* 2009; Catry *et al.* 2011; Limiñana *et al.* 2012b). Since itinerancy has even been proven for highly aerial swifts (Common Swift (Åkesson *et al.* 2012), Pallid Swift (Norevik *et al.* 2018)), there remain no species we believe to be really nomadic during their non-breeding period in Africa. Montagu's Harriers had been suspected to be nomadic, too (García & Arroyo 1998), before evidence of their itinerant movements had been gathered by satellite tracking (Trierweiler *et al.* 2013). Even though a species turns up in higher numbers when food abundance is high, this not necessarily means that it is erratic. Our harriers also sometimes added or skipped sites and adjusted their length of stay at a site according to environmental conditions in different years. This could mean that more birds stay longer in an area in a year with high food abundance compared to other years, leading to biased observations at single locations, which emphasizes the value of year-round tracking of individuals.

Montagu's Harriers used on average three distinct wintering sites. Most species seem to use a small number of sites during one winter (two in Red-backed Shrike (Tøttrup *et al.* 2012b, 2017), three in Thrush Nightingale (Stach *et al.* 2012), two or three in Common Swift (Åkesson *et al.* 2012), four in Common Cuckoo (Willemoes *et al.* 2014)). The number of sites depends to some extent on the definition of a stay at a site. Some authors call shorter visits "stopovers". This is often used in species that shift sites over large distances, also referred to as the second leg of migration (e.g. Red-backed Shrike (Tøttrup *et al.* 2012b)). We here decided to classify all sites where a bird stayed at least 3 days in the same area south of 18.5°N as a wintering site. However, this might have led to a higher number of wintering sites than when only considering stays of two or more weeks. Nevertheless, the repeated use of sites within and between years, including sites that were used for shorter periods, encouraged us to consider all of these visits and sites for our analyses.

Few species have proven to show a strategy of winter residency using only a single wintering site for the entire wintering period (Osprey (Kjellén *et al.* 1997; Alerstam *et al.* 2006), Common Redstart (Kristensen *et al.* 2013), Northern Wheatear (Schmaljohann *et al.* 2012), and Pied Flycatcher (Ouwehand *et al.* 2016). In other species, the majority of individuals is winter resident at a single site (e.g. Honey Buzzard *Pernis apivorus* (Hake *et al.* 2003), 10 out of 12 European Nightjar (Norevik *et al.* 2017), 17 out of 19 European Hoopoes (Bächler *et al.* 2010; van Wijk *et al.* 2016)). Mixed winter strategies exist in which some individuals use one residency site whereas others use two or more sites (e.g. 6 out of 9 Lesser Kestrels (Catry *et al.* 2011; Limiñana *et al.* 2012b), 3 out of 5 Turtle Doves (Eraud *et al.* 2013), 44 out of 66 Barn Swallows *Hirundo rustica* (Liechti *et al.* 2015), 25 % in Great Reed Warblers (Koleček *et al.* 2018), 1 out of 6 Tawny Pipits (Briedis *et al.* 2016)). In our case, only 3% of tracks (n = 4) showed a single wintering site. It has been suggested that food specialists are in higher need of itinerancy than generalists, as the latter could use various resources at the same site (Salewski *et al.* 2002), but too little is still known about the specific diets of the species involved to support this notion.

On average, consecutive sites of tracked harriers lay further southwards. Nevertheless, they stayed within the Sahel, using first sites in the northern Sahel savannahs, then shifting southwards into the Sudan and sometimes Guinea savannahs. Few species show itinerancy only within the Sahel. These are habitat specialists like the Tawny Pipit that stays only in the dry parts of the Sahel region (Briedis *et al.* 2016). Montagu's Harriers also prefer open landscapes and are therefore bound to the Sahel since more southern zones are too wooded. This is especially true in West Africa and we do not yet know how individual movement patterns of Montagu's Harriers wintering in East Africa or even India look like. In the Great Reed Warbler, individuals from a central European breeding population move southwards within West Africa, whereas individuals from a south-eastern European breeding population moved further south into central Africa (Koleček *et al.* 2018). The same is true for the Common Nightingale being itinerant within West Africa (Hahn *et al.* 2014) and the closely related Thrush Nightingale in East Africa moving much further south to their last wintering sites (Stach *et al.* 2012). Many other species use the Sahel in the beginning of the winter, just after the rainy season has ended and vegetation is still green and food plenty (Morel 1973). They then move on to more southern vegetation zones, e.g. Common Nightingales (Hahn *et al.* 2014) and Great Reed Warblers from central European breeding populations (Koleček *et al.* 2018), or even further south to enter central or southern Africa, e.g. Great Snipe (Lindström *et al.* 2016), European Nightjar (Norevik *et al.* 2017), Common Swift (Åkesson *et al.* 2012), Thrush Nightingale (Stach *et al.* 2012), and Red-backed Shrike (Tøttrup *et al.* 2012b).

Montagu's Harriers profit from the vegetation and food in the northern Sahel upon arrival in September. At these first sites, they stay on average for about one month. Then, using up to several intermediate sites, they move in general southwards to their last wintering site, but variation between individuals is large (cf. Fig. 2.2). The last site is for most individuals where they stay longest and where they prepare for spring migration. They stay at this last site for on average 3.5 months during which the environment gradually deteriorates. In response, harriers increase their hunting effort and consequences of habitat quality on departure date were observed (Schlaich *et al.* 2016). If the harriers moved directly to their last sites, they would not only miss the food peak in the north but could even arrive too early further south when conditions there might not yet be suitable. The observed re-use of sites within one winter, going back and forth between the same sites, suggests that the birds indeed occasionally sample sites, and arrive too early at a consecutive site. We have even anecdotic evidence that harriers make round trips from their actual site to sample the conditions at sites they will use later in the season. Re-use of sites was also documented in Lesser Spotted Eagles which re-visit several sites within a winter (Meyburg *et al.* 2015). These movements between known sites suggest again a flexible behaviour in adjustment to local environmental conditions.

Habitat composition and preferences

Wintering sites of harriers were composed of habitats ranging from sparsely vegetated to mainly agricultural habitats. In general, they preferred mosaic habitats consisting of grassland, cropland, shrubland, and sparse vegetation. This has been described before using satellite tracking and during field studies (Limiñana *et al.* 2012c; Trierweiler *et al.* 2013; Augiron *et al.* 2015). Here we focused on the differences between first, intermediate and last sites. More than three quarter of first sites was dominated by natural and sparse vegetation habitat categories of the northern Sahel savannahs, just south of the Sahara Desert. At intermediate and last sites, i.e. the greatest part of the wintering period, half of the sites was dominated by agriculture and mixed agricultural landscapes. This increase in the percentage use of agriculture does not reflect an increase in selectivity or a shift in habitat preferences, but rather higher availability of agricultural habitats at more southern latitudes.

Harriers preferred sites with higher habitat diversity, which is comparable to the breeding period (Trierweiler 2010). In general, diverse habitats host more biodiversity (Rosenzweig 1995) and therefore potentially more prey. Intensive monocultures may host high densities of a single prey species at a time, but might not be stable food sources. For example, the relative intensively farmed area of Khelcom in Senegal hosts high grasshopper numbers (Mullié & Guèye 2010) and big communal harrier roosts are at times observed in this area (Augiron *et al.* 2015; own observations). However, food availability might be more stable in small scale landscapes consisting of diverse habitats.

Just a few years ago, the analysis of tracking data made a major step forward due to the combination with remote sensing environmental data. In the case of Montagu's Harriers, Trierweiler *et al.* (2013) used vegetation greenness (NDVI) to explain why the birds are itinerant by showing that their wintering sites lay in a range of NDVI values that coincided with highest food abundance (grasshoppers) in the field, leading to the 'green belt hypothesis'. Trierweiler *et al.* (2013) also investigated habitat selection using the GlobCover land use map. Here, we used the same maps to determine environmental variables. However, despite tracking devices having greatly improved in precision and data quantity, the resolution of environmental maps has remained stable. Therefore, analysing habitat preferences within the individual home range are still limited by the temporal and especially spatial resolution of environmental data.

Another limitation is the accuracy and ecological relevance of habitat categories. The GlobCover land use map has an accuracy of 73% when compared to ground-truthing (Defourny *et al.* 2009). Furthermore, the categories could describe different habitats in different landscapes. For example, the category *sparse vegetation* was used more than available at first, intermediate and last sites. However, *sparse* at first sites are mainly sparsely vegetated grassy savannahs, whereas it includes estuaries (e.g. Sine Saloum) as well as laterite plateaus at intermediate and last sites. These habitats could host very different prey species and be used differently by harriers. Laterite plateaus have been noticed as important landscape structures often used by wintering harriers (own observations), since shrubs on these plateaus host grasshoppers and human disturbance is limited due to barren soil. Unfortunately, we cannot prove the importance of these landscape structures with our analysis because the laterite plateaus are not identifiable on the land use map. Visual inspection of known sites showed that classification on GlobCover ranges from *bare* to *mosaic vegetation/cropland*, making it impossible to estimate their importance. Future research using higher resolution maps with detailed habitat categories is important to gain conservation relevant information since these might be parts that could be protected without affecting human land use.

Vegetation greenness is often assumed to be a proxy of food availability. Since Montagu's Harriers mainly prey on grasshoppers during winter and grasshoppers depend on green vegetation, this is a valid, but rather rough approximation. Indeed, most harriers winter within the range of highest grasshopper abundance (Trierweiler *et al.* 2013). However, vegetation greenness cannot explain all and is not an absolute measure of grasshopper abundance. For example, some species of shrubs carry green leaves but host no grasshoppers at all. The same has been shown for tree-dwelling passerines; tree species vary largely in abundance of wintering Palearctic migrants, thus even though areas seem to be rich in trees this does not necessarily mean that these are trees used by migrants (Zwarts *et al.* 2015). In addition, other factors may influence grasshopper abundance, since their development depends not only on the actual local conditions but also on previous conditions. Other prey which are not that closely related to NDVI might serve as alternative prey. And last but not least, competition for prey might be an important factor. Not only from conspecifics (communal roosts of up to 4000 harriers have been observed) but also from many other species (local and Palearctic migrants) preying on grasshoppers. Furthermore, we do know much less about the first sites in the northern Sahel, since these have not yet been visited in the field (in contrast to more southern sites where grasshopper abundance was measured on the ground, (Trierweiler *et al.* 2013; Schlaich *et al.* 2016)). These northern sites might be ecologically different, with other vegetation and grasshopper species involved. Thus, NDVI is a coarse measure of habitat quality and food abundance and future studies addressing habitat quality and carrying capacity must investigate the underlying relations in more detail in the field, not only at intermediate and last sites but especially also at first sites.

Home range size and activity measures

Our calculated median total site home range size of 35 km^2 was much smaller compared to the estimates of about 200 km^2 from Trierweiler *et al.* (2013). The latter were estimated from satellite tracks with few positions. Here we only used the GPS tracks with much more and accurate positions. Furthermore, our estimates are based on a state-of-the-art method, the Biased Random Bridge Movement Model (BRBMM), that takes movements along the track into account, which is more advanced than considering the GPS positions as single unrelated observations. Therefore, we consider the previous estimate of home range size highly overestimated. Unfortunately, the method did not work for the calculation of daily home ranges. As alternative, we calculated non-movement-based kernel estimates of daily home ranges. Nevertheless, mean daily home range size (first sites 29 km^2, intermediate 26 km^2 and last 51 km^2) was in the same order of magnitude as the total site home ranges calculated with BRBMM (first sites 40 km^2, intermediate 21 km^2 and last 101 km^2). Daily home range size increased from first to last sites, as did the time spent flying per day and the daily distance covered. The daily estimates are dependent on the number of positions, and thus the GPS registration interval. However, within an individual, GPS-positions were recorded at the same interval during the whole winter, making daily measures comparable.

Total site home range size was larger for sites in drier areas. This is consistent with earlier findings that individuals at drier sites fly more and have larger home ranges (Schlaich *et al.* 2016).

Site fidelity

Bird ringing provided the first proof of recurrence or winter site fidelity, the faithfulness of individual migrants to wintering sites in subsequent years. Moreau (1969, 1972) summarized the first evidence that such faithfulness to a wintering site is widespread in a broad range of passerine and wader species. These first observations resulted from bird ringing projects in several African countries resulting in quite some recoveries in one or several years after first capture (Moreau 1972: Table XIX and XX on pages 260/261). In 2000, records of recurrence in Africa existed for 60 bird species (Sauvage *et al.* 1998; Salewski *et al.* 2000; King & Hutchinson 2001). Recent studies found high site fidelity by intensive field studies, e.g. in Whinchat (Blackburn & Cresswell 2016b), and thanks to tracking data, e.g. Lesser Spotted Eagle (Meyburg *et al.* 2015). Low site fidelity between wintering seasons has been documented in White Stork (Berthold *et al.* 2002, 2004), European Hoopoe (van Wijk *et al.* 2016), and Common Redstart (Kristensen *et al.* 2013). Until now, there are only few species where individuals are tracked in multiple years.

Montagu's Harriers showed strong site fidelity, using 75% of their wintering sites used in one winter also during the next winter. They were even more faithful to last wintering sites which they re-used in 90% of cases during the next winter. Recurrence at distinct sites comes with the advantage of local knowledge on food availability, water, predators, roosts etc. This might explain why many species are site faithful even though they are itinerant. They profit from local knowledge at several sites.

A notable exception of a Montagu's Harrier with no site fidelity was an individual which used a single wintering site in one year, and no less than five other sites in the subsequent year. This example seems a true exception, possibly caused by the loss of the original wintering site.

Inter-individual variation

In general, the harriers move southwards during the winter while the Sahel dries out, until they reach the southern border of this biome. However, we would like to stress that a notable variation exists in movement patterns between individuals. This is not only apparent from the variation in the number of sites used during the winter (from 1 to 6 sites), but also the variation in timing and duration of site use (Fig. 2.2), and the directions and distances birds move between sites. It was only possible to sketch this variation thanks to the large number of individuals we tracked. Although the inter-individual variation in movements of Montagu's Harriers might be relatively large compared to other species (e.g. Red-backed Shrike (Tøttrup *et al.* 2012b, 2017)), this variation nevertheless underlines that we need to be careful extrapolating from small sample sizes, an issue in many tracking studies. The large inter-individual variation in winter movements suggests a great flexibility of harriers to adjust to variation in environmental conditions.

Intra-tropical movements – within-individual responses to environmental variation

By using repeated tracks, we showed a within-individual response in flight distance per day to vegetation greenness, but home range size and number of flight hours were unrelated to vegetation greenness. Thus, a harrier at the same site in a drier year, while utilizing the same home range, travels more within this home range, maybe using a different hunting strategy or hunting on different prey items. To investigate these relations, fieldwork at a large scale is unavoidable.

Timing of movements between sites was often a flexible individual response to prevailing conditions. An individual stayed shorter at a first site and departed earlier from a first site in a drier year compared to a greener year. This seems in line with the above described idea that migrants profit from the food abundance in the northern Sahel upon arrival before moving southwards when conditions there start to deteriorate. The duration of stay at intermediate sites was not explained by vegetation greenness. However, this might be due to a changing number of intermediate sites or because conditions are not that influential at that moment. Arrival at last sites however, had a strong tendency to be earlier in greener years, and thereby, harriers can profit from good conditions at their most important site. With the 'green belt hypothesis', Trierweiler *et al.* (2013) formulated the idea that Montagu's Harriers stay within a certain range of NDVI values that indicate highest food abundance. We now showed that this is due to flexible adjustment of individuals to local environmental conditions. To date, only few studies correlated intra-tropical movements with environmental conditions. Mid-winter movements improved wintering conditions in Common Cuckoos (Thorup *et al.* 2017), Pallid Swifts (Norevik *et al.* 2018), Thrush Nightingales (Thorup *et al.* 2017), Great Reed Warblers (Koleček *et al.* 2018), Willow Warblers (Lerche-Jørgensen *et al.* 2017), and Red-backed Shrikes (Thorup *et al.* 2017). But to our knowledge, no other studies describe *intra-individual* responses in timing of intra-tropical movements to between year environmental variation, which we here did for Montagu's Harriers using a large tacking dataset with many individuals tracked in several years.

Future prospects

Recurrences of Great Reed Warbler individuals at the same site in Congo but at different times in subsequent years let Moreau (1972) to the question: 'How far, one wonders, is it the rule for these intra-tropical movements to be replicated in the successive seasons when they finally came to anchor in the same few square meters of African vegetation?'. Our results give first answers to his questions regarding Montagu's Harriers. Confirming that they are itinerant and showing high site fidelity, we showed that these migrants indeed replicate their intra-tropical movements but adjust the timing to environmental conditions. However, many open questions remain. We do not yet know what the consequences of this strategy are for the rest of the annual cycle. Earlier work hinted on carry-over effects with individual Montagu's Harriers departing later from drier sites than birds from greener sites and thus arriving later at the breeding grounds (Schlaich *et al.* 2016). However, these are between-individual differences and future analyses must elaborate on within-individual differences in timing through the whole annual cycle and the carry-over effects involved. Furthermore, we do not know if conditions at the breeding sites or wintering sites are limiting populations of Montagu's Harriers and how this varies between populations. And last, we do not yet understand how individuals develop these strategies. Very few studies have tracked juvenile birds as first year mortality is high and tracking expensive. For Honey Buzzards it has been shown that they are nomadic in their first winter but use distinct wintering sites as adult birds (Strandberg *et al.* 2012). This indicates that immatures might prospect future wintering sites over a larger region. Montagu's Harriers use communal roosts and thus could use social cues which might also influence immature decisions to stay or move on. In addition, some immatures spend their first summer in Africa. We need to investigate immature movements and site use in subsequent years in the future. This is necessary to understand the species' distribution at the wintering grounds which might help in future conservation efforts. Our results suggest that good wintering sites are important because birds at drier sites have to work harder and this might carry-over to later annual cycle stages. The choice of wintering sites, especially the last one, is therefore considered to be very important.

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Supplemental material

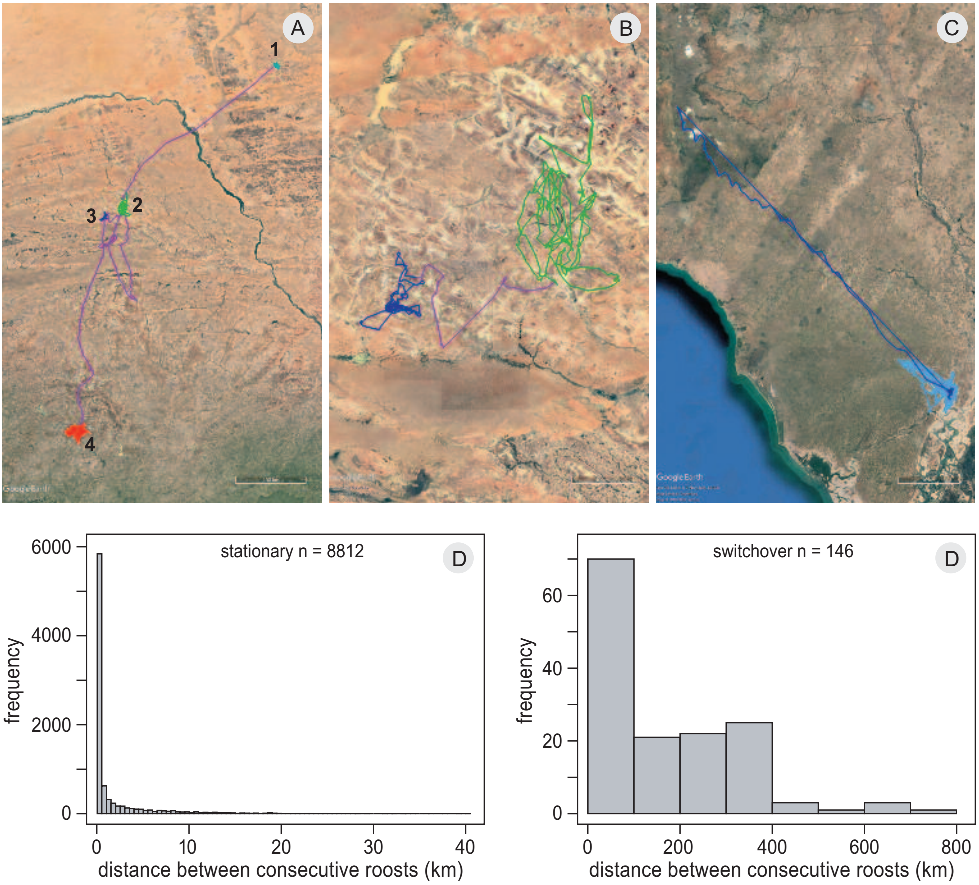

Figure S1. Annotation of tracking data. (**A**) Example of one winter of Dutch male Elzo in 2010/2011 using four consecutive wintering sites. Switchovers – movements between stationary wintering sites – are shown in purple. (**B**) Zoom to wintering sites 2 and 3 of the same bird. Sites are only separated by about 20 km but are clearly distinct with no overlapping tracks. (**C**) Example of a trip – explorative movement outside a distinct wintering site with return to the same site, here from Edwin in winter 2014/2015. Below: Frequency distribution of distances between consecutive roosts at stationary wintering sites (**D**) and for switchovers between sites (**E**).

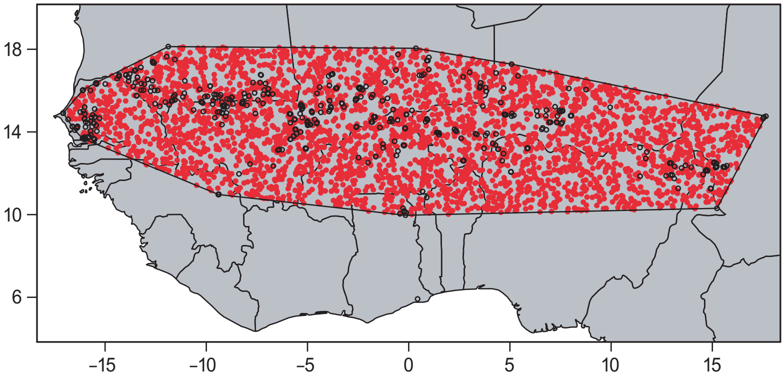

Figure S2. Random points (red) and centroids of Montagu's Harrier wintering sites (N = 450 sites, open black circles) within 100% MCP of all wintering sites (black line) used as available habitat in wintering range in West Africa.

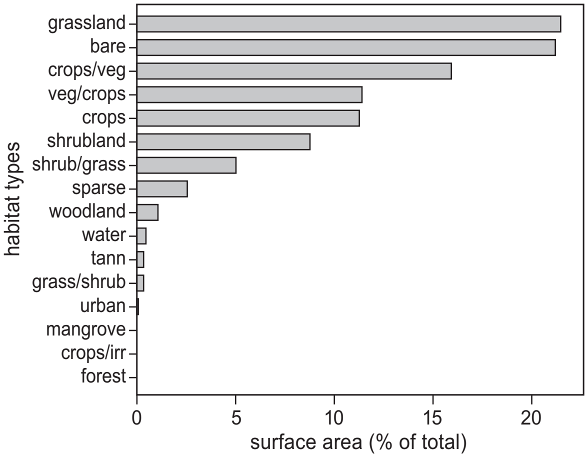

Figure S3. Availability of GlobCover land use categories in the whole wintering zone of our GPS- and satellite-tracked Montagu's Harriers (3295 random points within 100% MCP, see Fig. S1).

Table S1. GlobCover land use categories.

GlobCover value	Short name	Group	Score factor	>5% in used	>5% in avail (rectangle)	>5% in avail (random points)	GlobCover label
11	crops/irr						Post-flooding or irrigated croplands (or aquatic)
14	crops	agriculture	13	x	x	x	Rainfed croplands
20	crops/veg	agriculture	12	x	x	x	Mosaic cropland (50–70%) / vegetation (grassland/shrubland/forest) (20–50%)
30	veg/crops	agriculture	11	x	x	x	Mosaic vegetation (grassland/shrubland/forest) (50–70%) / cropland (20–50%)
40	forest						Closed to open (>15%) broadleaved evergreen or semi-deciduous forest (>5m)
50							Closed (>40%) broadleaved deciduous forest (>5m)
60	woodland	natural	10				Open (15–40%) broadleaved deciduous forest/woodland (>5m)
70							Closed (>40%) needleleaved evergreen forest (>5m)
90							Open (15–40%) needleleaved deciduous or evergreen forest (>5m)
100							Closed to open (>15%) mixed broadleaved and needleleaved forest (>5m)
110	shrub/grass	natural	9	x	x	x	Mosaic forest or shrubland (50-70%) / grassland (20–50%)
120	grass/shrub	natural	8				Mosaic grassland (50-70%) / forest or shrubland (20–50%)
130	shrubland	natural	7		x	x	Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m)
140	grassland	natural	6	x	x	x	Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)
150	sparse	sparse	5	x			Sparse (<15%) vegetation
160							Closed to open (>15%) broadleaved forest regularly flooded (semi-permanently or temporarily) - Fresh or brackish water
170	mangrove	sparse	4				Closed (>40%) broadleaved forest or shrubland permanently flooded - Saline or brackish water
180	tann	sparse	3				Closed to open (>15%) grassland or woody vegetation on regularly flooded or waterlogged soil - Fresh, brackish or saline water
190	urban						Artificial surfaces and associated areas (Urban areas >50%)
200	bare	sparse	2	x	x	x	Bare areas
210	water	sparse	1				Water bodies
220							Permanent snow and ice
230							No data (burnt areas, clouds,…)

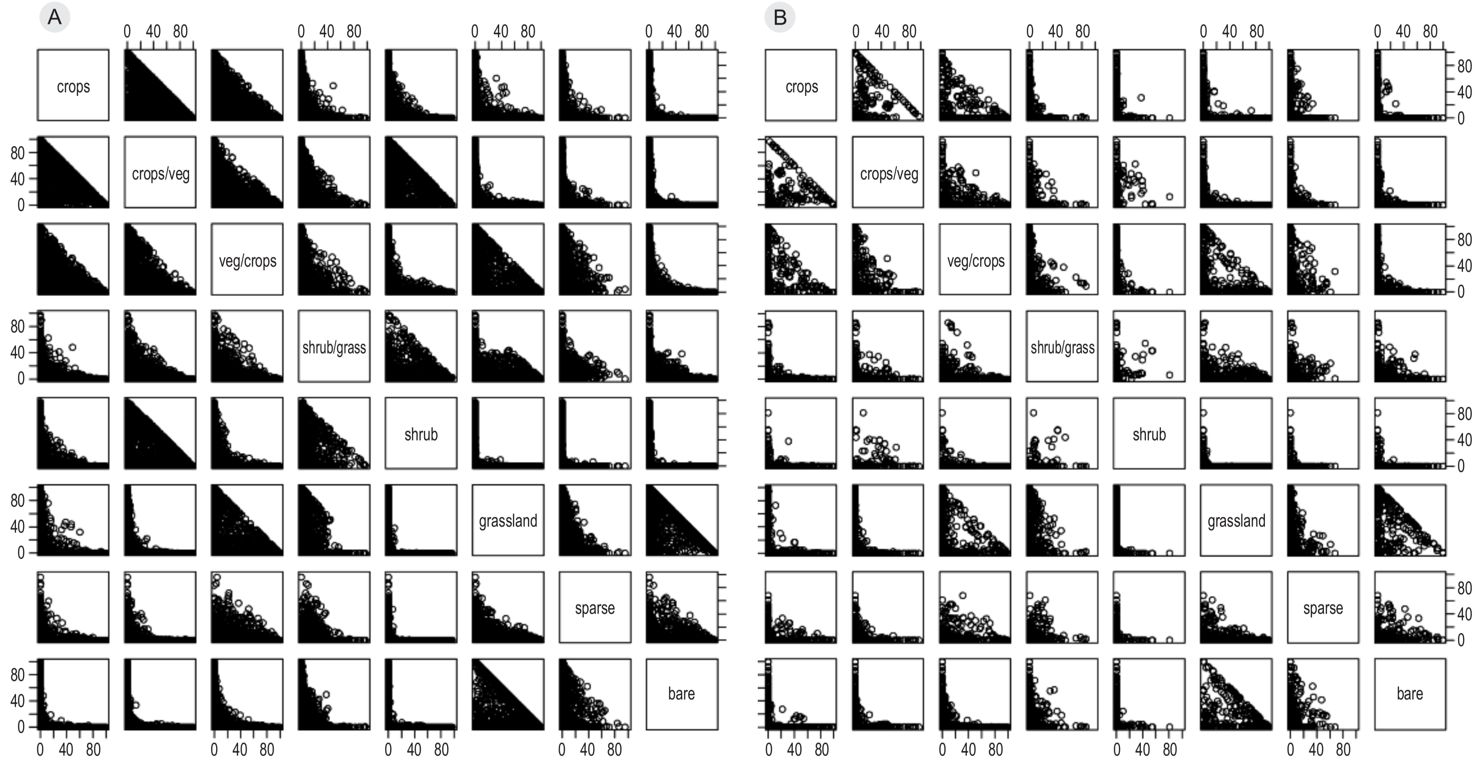

Figure S4. Correlations between most abundant habitat categories (>5% surface area or use) at (**A**) random points within 100% MCP of all harrier wintering sites (n = 3295) and (**B**) harrier wintering sites (n = 450). These subsequent habitat types were spatially correlated and form a gradient from north to south with increasing vegetation cover and agricultural productivity. Habitat types that are close to each other substitute each other whereas habitat types at the ends of the gradient exclude each other.

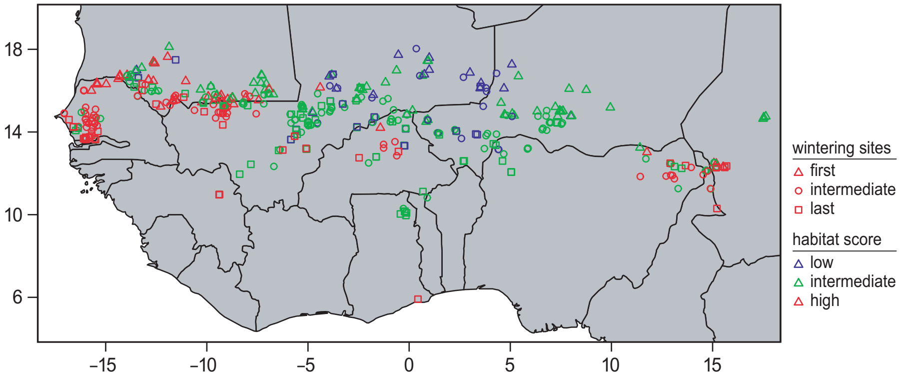

Figure S5. Wintering sites of GPS and satellite tracked Montagu's Harriers (n = 129 sites) coloured according to habitat score groups (low <5.6, intermediate 5.6 – 9.2, high >9.2).

Table S2.

Bird name	Winter	Bird name	Winter	Bird name	Winter
Cathryn	2006/2007	Pieter	2011/2012	Lea	2013/2014
Merel	2006/2007	Yde	2011/2012	Tineke	2013/2014
Franz	2007/2008	Dominik	2011/2012	Viviane	2013/2014
Doris	2007/2008	Hanna-Luise	2011/2012	Ronny	2014/2015
Edzard	2007/2008	Mathilde	2011/2012	EllenMargrete	2014/2015
Fenna	2007/2008	Tineke	2011/2012	F1020f	2014/2015
Grazyna	2007/2008	Edwin	2012/2013	F1018f	2014/2015
Halina	2007/2008	Pieter	2012/2013	Tim	2014/2015
Jinthe	2007/2008	F666m	2012/2013	Cornelis	2014/2015
Merel	2007/2008	F578m	2012/2013	Hinrich	2014/2015
Volia	2007/2008	Marc	2012/2013	Asbjoern	2014/2015
Franz	2008/2009	F837m	2012/2013	Astrid	2014/2015
Cathryn	2008/2009	Ronny	2012/2013	Hanna-Luise	2014/2015
Dominik	2008/2009	F838m	2012/2013	Henry	2014/2015
Grazyna	2008/2009	Jannie	2012/2013	Leen	2014/2015
Merel	2008/2009	JanGerard	2012/2013	Ludmila	2014/2015
Tania	2008/2009	Morri	2012/2013	Mark	2014/2015
Volia	2008/2009	F843f	2012/2013	Viviane	2014/2015
Edwin	2009/2010	Flemming	2012/2013	Yura	2014/2015
Willem	2009/2010	Inga	2012/2013	Cornelis	2015/2016
Alexandre	2009/2010	Floortje	2012/2013	Hinrich	2015/2016
Franz	2009/2010	Corry	2012/2013	FokkoJohannes	2015/2016
Dominik	2009/2010	Astrid	2012/2013	Astrid	2015/2016
Grazyna	2009/2010	Hanna-Luise	2012/2013	Kees	2015/2016
Iben	2009/2010	Lea	2012/2013	Ludmila	2015/2016
Mathilde	2009/2010	Mathilde	2012/2013	Mark	2015/2016
Michael	2009/2010	Tineke	2012/2013	Roger	2015/2016
Remt	2009/2010	Edwin	2013/2014	Rowan	2015/2016
Volia	2009/2010	Ronny	2013/2014	Yura	2015/2016
Rita	2010/2011	Jannie	2013/2014	Hinrich	2016/2017
Elzo	2010/2011	F843f	2013/2014	Arion	2016/2017
Franz	2010/2011	Flemming	2013/2014	Astrid	2016/2017
Dominik	2010/2011	Floortje	2013/2014	Beatrice	2016/2017
Hanna-Luise	2010/2011	F746m	2013/2014	Ludmila	2016/2017
Iben	2010/2011	F829m	2013/2014	Mark	2016/2017
Jo	2010/2011	Laurens	2013/2014	Roger	2016/2017
Joern	2010/2011	EllenMargrete	2013/2014	Sally	2016/2017
Klaus-Dieter	2010/2011	Joey	2013/2014	Arion	2017/2018
Mathilde	2010/2011	F1019f	2013/2014	Beatrice	2017/2018
Michael	2010/2011	F1020f	2013/2014	James	2017/2018
Tineke	2010/2011	Astrid	2013/2014	John	2017/2018
Edwin	2011/2012	Hanna-Luise	2013/2014	Ludmila	2017/2018
Elzo	2011/2012	Henry	2013/2014	Ruth	2017/2018

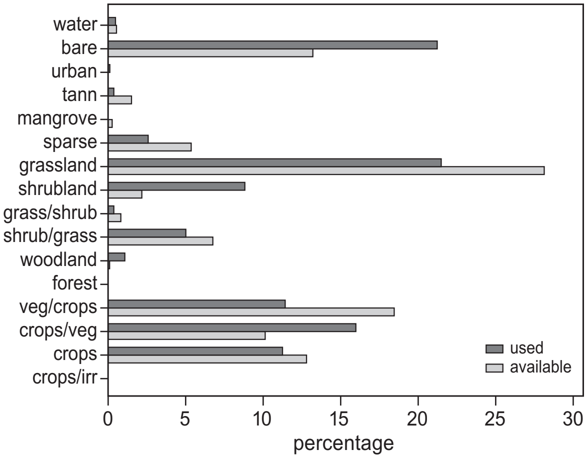

Figure S6. Habitat preferences for Montagu's Harriers' wintering sites compared to the available habitats in the whole wintering range at random points (n = 3295) within the 100% MCP of the tracked birds.

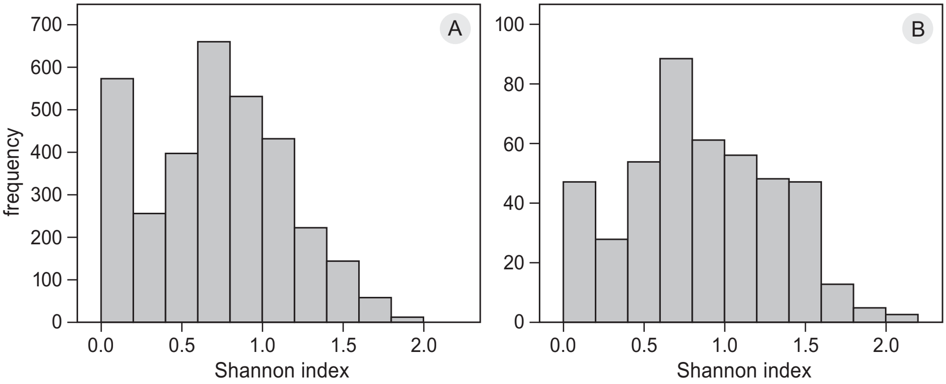

Figure S7. Habitat diversity calculated as Shannon's diversity index at (**A**) random sites (n = 3295) and (**B**) harrier wintering sites (n = 221).

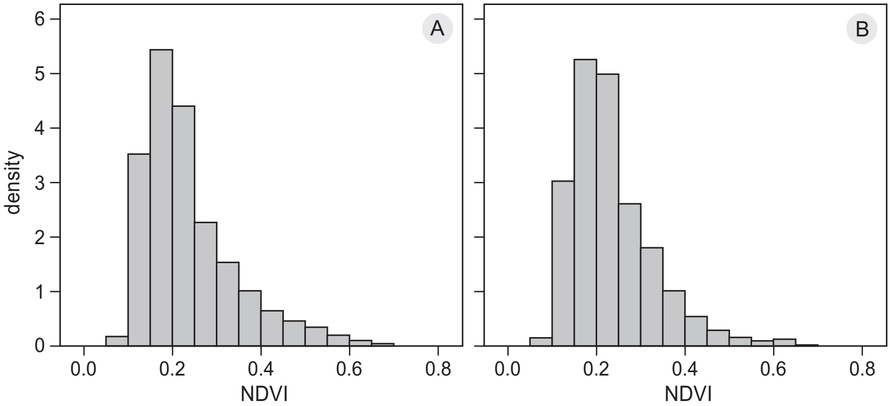

Figure S8. NDVI (Normalized Difference Vegetation Index) at (**A**) random sites (n = 750) and (**B**) harrier wintering sites (n = 450) on three dates (30 Sep, 1 Nov, 6 Mar) during the winters 2006/2007 till 2017/2018.

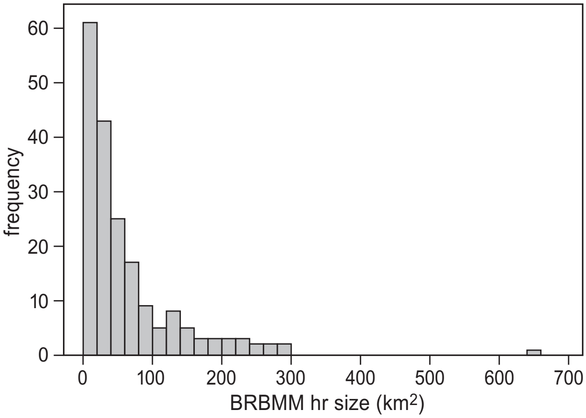

Figure S9. Home range size of Montagu's Harrier wintering sites (n = 193) calculated with the Biased Random Bridge Movement Model.

3

How individual Montagu's Harriers cope with Moreau's Paradox during the Sahelian winter

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Summary

1. Hundreds of millions of Afro-Palaearctic migrants winter in the Sahel, a semi-arid belt south of the Sahara desert, where they experience deteriorating ecological conditions during their overwintering stay and have to prepare for spring migration when conditions are worst. This well-known phenomenon was first described by R.E. Moreau and is known ever since as Moreau's Paradox. However, empirical evidence of the deteriorating seasonal ecological conditions is limited and little is known on how birds respond.
2. Montagu's Harriers *Circus pygargus* spend 6 months of the year in their wintering areas in the Sahel. Within the wintering season, birds move gradually to the south, visiting several distinct sites to which they are site-faithful in consecutive years. At the last wintering site, birds find themselves at the southern edge of the Sahelian zone and have no other options than facing deteriorating conditions.
3. We tracked 36 Montagu's Harriers with GPS trackers to study their habitat use and behaviour during winter and collected data on the abundance of their main prey, grasshoppers, in Senegal. Since grasshopper abundance was positively related to vegetation greenness (measured as normalized difference vegetation index, NDVI), we used NDVI values as a proxy for prey abundance in areas where no field data were collected. Prey abundance (grasshopper counts and vegetation greenness) at wintering sites of Montagu's Harriers decreased during the wintering period.
4. Montagu's Harriers responded to decreasing food availability by increasing their flight time during the second half of the winter. Individuals increased flight time more in areas with stronger declines in NDVI values, suggesting that lower food abundance required more intense foraging to achieve energy requirements. The apparent consequence was that Montagu's Harriers departed later in spring when their final wintering site had lower NDVI values and presumably lower food abundance and consequently arrived later at their breeding site.
5. Our results confirmed the suggestions Moreau made 40 years ago: the late wintering period might be a bottleneck during the annual cycle with possible carry-over effects to the breeding season. Ongoing climate change with less rainfall in the Sahel region paired with increased human pressure on natural and agricultural habitats resulting in degradation and desertification is likely to make this period more demanding, which may negatively impact populations of migratory birds using the Sahel.

Introduction

Each autumn, hundreds of millions of Palaearctic migratory birds head south to spend the winter in more favourable conditions closer to the equator. However, ecological conditions in the Sahel, the semi-arid belt south of the Sahara desert and a zone used by many sub-Saharan migratory species for overwintering (Zwarts *et al.* 2009), seem not to be all that beneficial. The Sahel is characterized by a rainy season usually lasting from June to October; hence migrants arrive during the best period (Morel 1973). However, from November to May the Sahel zone dries up continually, and thus ecological conditions deteriorate during the wintering stay of migratory birds (Zwarts *et al.* 2009). Moreau was one of the first to wonder how all the Palaearctic migrants could (i) sustain themselves in the Sahel and (ii) prepare for spring migration in environmental conditions that are continuously deteriorating during their stay (Moreau 1972). This is the so-called Moreau's Paradox, which was widely embraced (e.g. Alerstam 1990; Fry 1992; Berthold 1993; Salewski *et al.* 2006; Rappole 2013). Twenty years later, Fry (1992) summarized the observations of Morel and Moreau and discussed partial resolutions of Moreau's Paradox: (i) the Sahel contains important wetlands, (ii) insect biomass in *Acacia* savannah continues to increase long after the rainy season (November), (iii) African native birds emigrate southward at the time migrants arrive, thus reducing competition, and (iv) insectivorous migrants can become frugivorous and feed on berries of widespread trees during winter and in preparation for spring migration. More recently, Zwarts *et al.* (2015) confirmed Moreau's Paradox: highest densities of insectivorous birds are reached in the most desiccated areas of West Africa where they are found in thorny tree species that are supposed to host high insect numbers. These findings suggest that there might be no paradox for certain species and explain why so many migrants spend the winter in the Sahel. However, so far there remain many questions on the second part of Moreau's Paradox: how can migrants prepare for spring migration if conditions are deteriorating during the wintering period. No studies have demonstrated whether prey availability really decreases, how wintering birds react to such changes, and whether this has consequences for individuals. In the past we have witnessed large declines in breeding population sizes in Europe of many migrants wintering in the Sahel, as a result of droughts in the 1970s and 1980s (Zwarts *et al.* 2009). The ongoing human pressure on these habitats (Vickery *et al.* 2014), together with the predicted declines in rainfall in this century (Hulme *et al.* 2001), continue to put pressure on these species.

In the northern Sahel the drying out starts earlier than in the south because rainfall is less and the dry season starts earlier (rainy season north: July-September; 300 km further south: June-October) (Zwarts *et al.* 2009). Therefore, birds initially wintering in the northern Sahel move southwards during the wintering season (e.g. Catry *et al.* 2011; Trierweiler *et al.* 2013). However, for many species that prefer open savanna landscapes, moving even further southwards at the end of their wintering season is not an option in the western Sahel since habitats further south become increasingly closed and forested. These species have to cope with deteriorating conditions and might adapt to this by changing space use. One could expect that birds which experience decreasing prey availability would increase foraging time or effort by either roaming further or increasing the time spent foraging within the same area, possibly also accompanied by a switch to other prey species. Recent technological advancements give us the possibility to investigate the behaviour of individual birds remotely. Using detailed GPS-tracking data we are able to calculate behavioural measures such as the time flying, the distance covered and area used on a daily basis.

Montagu's Harriers *Circus pygargus* spend more than 6 months in the Sahel (Trierweiler & Koks 2009). Satellite tracking of individual birds has revealed that they are itinerant using distinct sites (on average four) to which they are site-faithful in consecutive years (Trierweiler *et al.* 2013). During the wintering season, sites are located progressively further southwards following a shifting 'green belt' of vegetation harbouring highest food abundance (Trierweiler *et al.* 2013). Wintering harriers prefer open landscapes and avoid forested areas (Limiñana *et al.* 2012a; Trierweiler *et al.* 2013; Augiron *et al.* 2015), thus lack the possibility to move further south when conditions continue to deteriorate during winter. From their last wintering site in the southern Sahel, birds depart directly north at the onset of spring migration (March). This means that they have to maintain themselves and prepare for migration within an area at the time of worst ecological conditions. Montagu's Harriers are acridivorous during the winter, feeding mainly on local grasshopper species (Mullié 2009; Trierweiler & Koks 2009; Mullié & Guèye 2010; Trierweiler *et al.* 2013). The most abundant grasshoppers during the dry season are species with diapausing adults, from mid-October onwards only adults are present which are depleted by predation during the season (Mullié 2009; Mullié & Guèye 2010).

The aim of our study was to investigate whether Moreau's Paradox is a real paradox for Montagu's Harriers, thus whether ecological conditions indeed deteriorate towards the end of their wintering period and how birds react to those changes. Therefore, we concentrate on the final wintering site where individuals reside before spring departure. We hypothesize that at this time and place, individuals experience deteriorating conditions. This may impact their foraging behaviour and even have carry-over effects to consecutive seasons. We predict that birds have to increase their foraging effort in response to decreasing prey abundance. To investigate this, we combine field data on prey availability collected at wintering sites in Senegal with high-resolution GPS-tracking data of Montagu's Harriers. Hence, our study provides a prime example of Moreau's Paradox, illustrated at the level of individual birds, giving insights into how migrants deal with deteriorating ecological conditions at the end of their wintering period.

Materials and methods

Study sites

In 2014 and 2015, we conducted fieldwork in five wintering areas of Montagu's Harriers in central-western Senegal, situated between 14.8°N and 13.6°N and 16.7°W and 15.4°W (Fig. 3.1A,B). 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. We considered 2014 a wet year since it was wetter than the 47 years before, and 2015 a dry year because it was

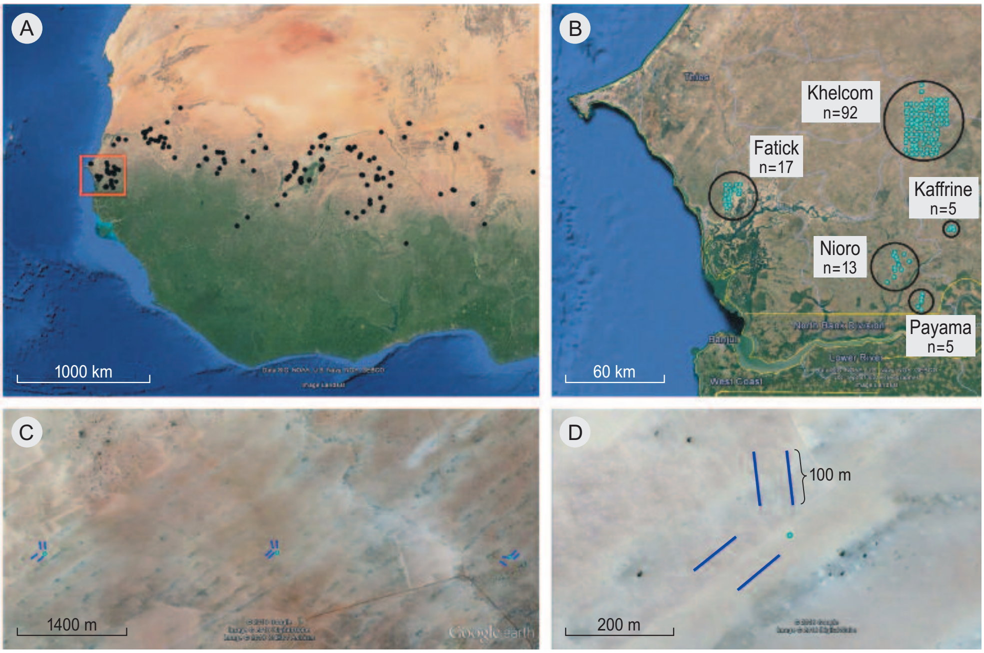

Figure 3.1. (**A**) Montagu’s Harrier wintering areas in the Sahel of West Africa. Black dots indicate wintering areas of GPS-tracked Montagu’s Harriers. An individual visits several consecutive areas during the winter, thus being reflected by multiple points on the map. The red rectangle encloses our study sites in Senegal. (**B**) Study sites in Senegal with sampling points for grasshopper transect counts marked in light blue. (**C**) Alignment of sampling points at approximately 3 km distance from each other, each surrounded by four transects. (**D**) Typical position of four grasshopper transects of 100 m length around sampling point.

drier than the last 16 years (Fig. S1, Supporting Information). Areas were chosen because GPS-tagged Montagu's Harriers from breeding populations in the Netherlands, Denmark, Germany and France were or had been using these areas as their last wintering sites. 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 5000 individuals (Mullié & Guèye 2010; Augiron *et al.* 2015). In Khelcom, individual roosts support between several hundred up to 4000 harriers (January 2015). This area consists of a mosaic of herbaceous savanna, fallow land and cropland [mainly groundnut *Arachis hypogaea* and millet *Pennicetum glaucum*; for a detailed description see Mullié & Guèye 2010]. The relatively high percentage of fallow land (Herrmann & Tappan 2013) 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 savanna 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 south-western 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, also 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 several up to 50 birds were observed.

Grasshopper transect counts

At the two main study sites, Khelcom and Fatick, we conducted grasshopper transect counts on a grid of sampling points at a distance of approximately 3 km to each other covering the core of the area used by GPS-tagged Montagu's Harriers (Khelcom n = 92 points, Fatick n = 17 points; Fig. 3.1B,C). The grid in Khelcom was considerably larger since more individuals were present in the area (of which some were tagged in this area). The other three sites were each the wintering site of a GPS-tracked harrier equipped on its breeding grounds. During the first visit in search of the birds, sampling points, mostly also with around 3 km distance between each other, were established in places that were used by the tracked individuals in the year before (Nioro n = 13, Kaffrine n = 5, Payama n = 5).

At each sampling point four transects, each of 100 m length, were walked by two observers with a minimal distance of 50 m between transects (Fig. 3.1D). For each transect the start and end positions were marked with a GPS during the first visit in January 2014. The same transects (with an accuracy of <10 m) were walked in the middle of the wintering season of harriers (end of January/ beginning of February) and at the end of the wintering season (end of March/beginning of April) in 2014 and 2015, respectively. Thus the same transects were counted twice per season in two consecutive years. Transects were in homogenous habitats, and habitat characteristics were noted on a standardized form (Appendix S1). All grasshoppers within 1 m each side of the transect line were counted. We distinguished two size categories of grasshoppers: less or equal to 3 cm or larger than 3 cm. Approximate grasshopper biomass was calculated by multiplying the encountered numbers by wet weights of the two most common grasshopper species observed in the area of Khelcom (Mullié & Guèye 2010; category small: *Acorypha clara*, 0.9 g; big: *Ornithacris cavroisi*, 2.6 g). Since the species encountered during transect counts depend on green vegetation we used normalized difference vegetation index (NDVI) as a proxy for food availability (cf. Trierweiler *et al.* 2013, see below).

GPS-tracking data of Montagu's Harriers

Between 2009 and 2015, we collected GPS-tracking data using UvA-BiTS GPS trackers (Bouten *et al.* 2013; www.uva-bits.nl) from 36 Montagu's Harriers (25 males and 11 females). Birds were captured during the breeding season in the Netherlands (53.2° N 7.2° E, n = 17), France (46.2° N 0.4° W, n = 8), and Denmark (55.1° N 8.7° E, n = 6), plus five at their wintering site in Senegal (Khelcom). One male captured in the Netherlands spent the three following breeding seasons in Germany (52.6° N 8.37° E). One Danish male stayed in Africa during one summer (Sørensen *et al.* 2017) and was removed from the data set for further analyses. Since several individuals were tracked in more than 1 year, the total number of year*individual combinations in the data set was 53. Of those, only 43 had complete data (in five cases the end of the winter was missing; in two cases the start was missing, and in three cases both the start and the end were missing). In addition, we excluded two individuals as insufficient data were collected per day to calculate daily measures, thus keeping, in total, 41 complete year*individuals. To analyse whether foraging behaviour changed during the individuals' stay at their last wintering site where they might experience deteriorating conditions within the same area, we considered only year*individual combinations where the bird stayed longer than 60 days at its last wintering site. Those summed up to 31 year*individual combinations. Arrival and departure at different wintering sites were determined visually (see Fig. S2 for an example), with the first wintering site being defined as the first site south of 18° N in which the bird stayed for at least 3 days. Start of spring migration and arrival date at the breeding site were also determined visually, with the first having been obvious in all cases, since birds stay in their wintering area until they abruptly head north (Fig. S2C).

The GPS loggers were programmed to collect GPS positions at an interval of 5 min (n = 2 tracks), 10 min (9), 15 min (16) or 30 min (4) during the day and at maximum once per hour during the night. Intervals differed because memory storage increased with newer trackers. Only positions during daylight were used for the analyses, with daylight being defined as being between nautical dawn and nautical dusk. By subsampling the 5-min interval data of one bird to intervals of 10, 15, 20 and 30 min, we checked whether the different daily measures were a function of the recording interval. Since this was not the case (data not shown), we only subsampled the 5-min interval data to 10-min intervals to keep three common intervals (10, 15 and 30 min). Data were checked for outliers visually and by calculating trajectory speed (between two consecutive GPS positions) and discarding points with trajectory speeds higher than 25 m s^{-1}.

Calculation of daily foraging parameters

Foraging parameters such as time spent flying, distance covered and home range size were calculated for each day. Days with fewer than 75% of expected positions (54 for 10-min interval, 36 for 15-min interval, and 18 for 30-min interval) were removed from the data set. Using instantaneous speed, we determined for each position if the bird was sitting or flying by means of a threshold of 1.2 m s^{-1} (local minimum of a two-peaked frequency distribution of speed values, see Fig. S3 for an example of a frequency distribution of instantaneous speeds). Time spent flying per day (in hours) was calculated as the percentage of positions spent flying in order to correct for length of day. Daily cumulative distance was calculated by summing up the distances between consecutive positions during each day. Distance between positions was calculated using function *distMeeus* from R package *geosphere* version 1.5-1 (Hijmans 2015). Daily home range size was calculated as 95% kernel density estimation

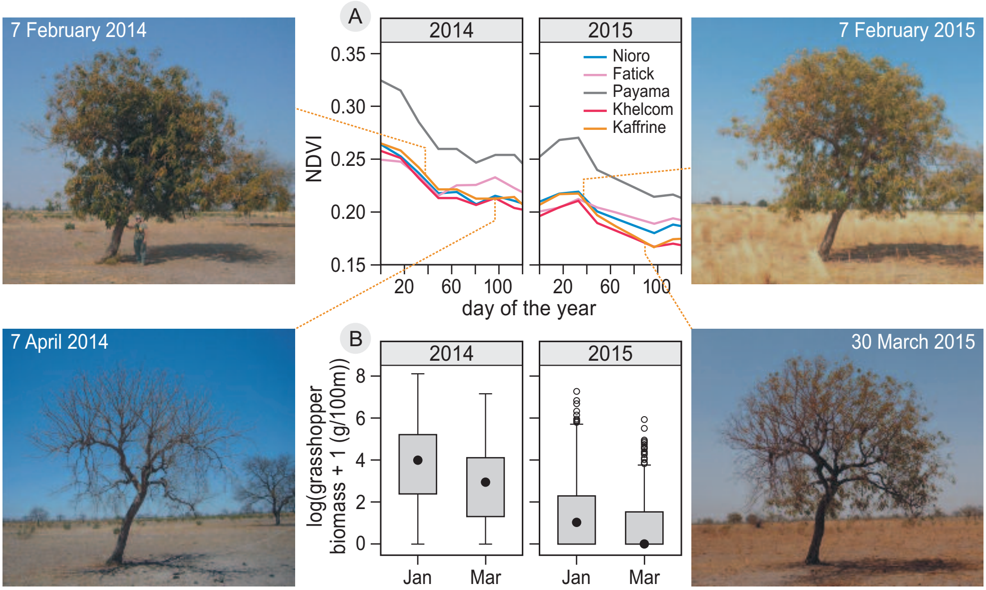

Figure 3.2. (**A**) Normalized difference vegetation index (NDVI) in five wintering areas of Montagu's Harriers in Senegal during the winters 2013/2014 and 2014/2015. Dashed lines indicate periods of fieldwork. Pictures were taken in area "Kaffrine". (**B**) Grasshopper biomass (log-transformed) in the middle (January) and at the end (March) of the wintering period of Montagu's Harriers in 2014 and 2015 in five areas in Senegal. n = 2193 transects of 100 m length.

using R package *rhr* version 1.2 (Signer & Balkenhol 2015). The bandwidth parameter *h* was determined by reference bandwidth estimation using function *rhrHref*.

Normalized difference vegetation index data

NASA's MODerate-resolution Imaging Spectroradiometer (MODIS) normalized difference vegetation index (NDVI) remotely sensed data (product MOD13Q1: data provided every 16 days at 250 m spatial resolution) were downloaded from The Land Processes Distributed Active Archive Center (LP DAAC – https://lpdaac.usgs.gov) using R package *MODISTools* (Tuck *et al.* 2014). Around each point of grasshopper sampling, 9 × 9 = 81 pixels of 250 × 250 m (~5 km^2) were downloaded for the years 2014–2015. The mean of those 81 pixels was calculated for each 16-day period, and the values for the period corresponding to the actual grasshopper count dates were added to the grasshopper transect data set. Mean NDVI at each study site (Fig. 3.2) was calculated by averaging the values of all sampling points in the area. No NDVI values could be retrieved for transects counted in March 2015 due to a gap in available NDVI data.

As grasshopper numbers were negatively correlated with NDVI (see Results), we used vegetation greenness as a proxy for grasshopper abundance in areas where no field data on grasshoppers were collected. Indeed, the abundance of grasshoppers will not strictly be determined by the greenness of the vegetation at the exact moment of the transect counts, but will also have been influenced for example by the amount of rainfall during the preceding rainy season, the greenness in the previous dry season or the number of grasshoppers in the previous year. Nevertheless, it has been shown that NDVI is a valuable tool to gain insight into trophic interactions on a global scale (Pettorelli *et al.* 2005), to locate potential grasshopper and locust habitats (Tappan *et al.* 1991; Waldner *et al.* 2015), and could be used as proxy for food availability (Szép & Moller 2005; Trierweiler *et al.* 2013).

For each wintering site of all GPS-tracked Montagu's Harriers, 25 × 25 = 625 pixels of 250 × 250 m (~39 km^2, mean home range size) around the mean latitude/longitude of that site were downloaded for the years the bird was present at that site. The average of the 625 pixels was calculated for each 16-day period and to each day of the harrier data set the value of the corresponding period was added.

Statistical analyses

All analyses were performed in R 2.15.2 (R Core Team 2014). Grasshopper abundance and biomass were log-transformed and modelled using linear mixed models (LMM) with *month* (January or March) and *year* (2014 or 2015) as fixed effects and *session* (2014.1, 2014.2, 2015.1 and 2015.2) and *transect ID* nested in *sampling point* and *area* as random effects by means of R function *lmer* from package *lme4* version 1.1-7 (Bates *et al.* 2015). Confidence intervals were retrieved using R function *confint.merMod* from the same package. The relation between grasshopper biomass (log-transformed) and NDVI was tested using a generalized additive mixed model (GAMM) with session and *transect ID* nested in *sampling point* and *area* as random effects by means of R function *gamm4* from package *gamm4* version 0.2-4 (Wood & Scheipl 2014). Changes in NDVI values during the stay of harriers at their final wintering site were modelled using a GAMM with *yea*r and *individual* nested in *year* as random effects. The trend of daily measures (time spent flying, cumulative distance and kernel home range size) over time, as well as the relation of time spent flying and NDVI, was also investigated by means of GAMMs with *year* and *individual* nested in *year* as random effects. The relation between departure date and NDVI, latitude of the final wintering site, breeding latitude and sex and the relation between arrival date and departure date, latitude of the final wintering site, breeding latitude and sex was tested using linear models (LM).

Results

Seasonal trends in food availability

Normalized difference vegetation index values in the five study areas in Senegal decreased over the course of the wintering period and were lower in the dry winter 2014/2015 than in the wetter winter 2013/2014 (Fig. 3.2A). We found that the abundance of grasshoppers decreased from January to March by 56% and 68% in the winters 2013/2014 and 2014/2015, respectively, and was lower in 2015 compared to 2014 (Table 3.1A, Fig. 3.2B; mean values in January and March: 2014 77.68 and 34.28, 2015 13.13 and 4.2). The same pattern was observed for biomass (Table 3.1B, Fig. 3.2B; mean values in January and March: 2014 181.49 and 60.09, 2015 23.36 and 7.21). Finally, grasshopper biomass was also positively correlated with NDVI values before reaching a plateau at higher NDVI values (Table 3.1C, Fig.

Table 3.1. Summary statistics of models on within-winter changes in grasshopper abundance and biomass, as well as Montagu's Harriers' behaviour at their last wintering site.

Variable	**Estimate**	**s.e.**	***t*–value**	**Lower CI**	**Upper CI**
(A) Grasshopper abundance (GLMM)					
Intercept	3.125	0.396	7.887	2.286	3.976
Month	–0.558	0.072	–7.704	–0.681	–0.434
Year	–1.767	0.072	–24.403	–1.890	–1.643
(B) Grasshopper biomass (GLMM, estimates shown in Fig. 3.2B)					
Intercept	3.674	0.495	7.421	2.665	4.695
Month	–0.715	0.196	–3.656	–1.027	–0.403
Year	–2.096	0.196	–10.718	–2.408	–1.784

	edf	***F*–value**	***P*–value**
(C) Grasshopper biomass (GAMM, estimates shown in Fig. 3.3)			
s(NDVI)	3.82	36.7	<0.001
(D) Seasonal NDVI changes in individual wintering area harriers (GAMM, Fig. 3.4B)			
s(date)	3.97	546.5	<0.001
(E) Seasonal pattern in hours flying per day for individual harriers (GAMM, Fig. 3.4D)			
s(date)	5.43	121.8	<0.001
(F) Hours flying per day for individual harriers in relation to local NDVI (GAMM, Fig. 3.4F)			
s(NDVI)	7.02	33.19	<0.001
(G) Seasonal pattern in cumulative distance per day flown by individual harriers (GAMM, Fig. S5B)			
s(date)	3.76	61.24	<0.001
(H) Seasonal pattern in kernel home range size of individual harriers (GAMM, Fig. S5D)			
s(date)	4.17	29.72	<0.001

	Estimate	**s.e.**	***t*–value**	***P*–value**
(I) Departure date from wintering grounds (LM, Fig. 3.5A)				
Intercept	81.598	24.115	3.384	0.003
NDVI	–42.8237	19.544	–2.191	0.040
Wintering latitude	–1.099	0.856	–1.283	0.210
Breeding latitude	0.587	0.339	1.733	0.097
Sex	–1.941	2.324	–0.835	0.413
(J) Arrival date at breeding grounds (LM, Fig. 3.5B)				
Intercept	40.295	25.069	1.607	0.120
Departure date	0.568	0.177	3.215	0.003
Wintering latitude	0.020	0.793	0.026	0.980
Breeding latitude	0.666	0.328	2.032	0.052
Sex	–1.907	2.076	–0.918	0.367

3.3), confirming both a seasonal decrease in grasshopper abundance and lower values during winter 2014/2015 compared to winter 2013/2014.

Foraging effort response of Montagu's Harriers to food availability

Montagu's Harriers tracked by GPS loggers were wintering in the Sahel between Senegal in the west and Niger in the east (Fig. 3.1A). At their final wintering site, birds experienced decreasing NDVI values during the course of their stay (Table 3.1D, Fig. 3.4A,B).

Montagu's Harriers flew, on average, between 2.25 and 8.43 (mean 4.98) hours per day at their final wintering site, and almost all individuals increased the amount of flight time gradually between January and spring departure at the end of March/beginning of April (Table 3.1E, Fig. 3.4C,D; for individual graphs see Fig. S4). On average, birds flew 1.74 times more during the last 10 days than during the first 10 days of their stay at their last wintering site, thus nearly doubling the time they spent flying. In addition, both cumulative daily distance (1.97 times, Table 3.1G, Fig. S5A) and kernel home range size (9.59 times, Table 3.1Hh, Fig. S5B) also increased between January and March.

Individuals increased their flight time when local NDVI values dropped at their final wintering site (Table 3.1F, Fig. 3.4E,F; for individual graphs see Fig. S6). The steepest increase in flight time was observed in the range of NDVI values in which grasshoppers were mostly affected in our Senegal data set (0.19–0.25, compare Figs 3.3 and 3.4E,F), suggesting that the increase in flight time was a direct response to declining prey densities. Montagu's Harriers departed later on spring migration when encountering lower NDVI values (Table 3.1I, Fig. 3.5A), and subsequently arrived later in their breeding area (Table 3.1J, Fig. 3.5B). Breeding latitude, latitude of the final wintering site and sex did not significantly contribute to these patterns.

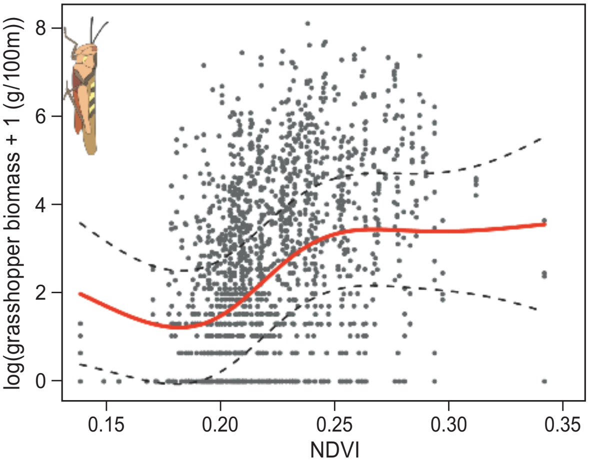

Figure 3.3. Grasshopper biomass (log-transformed) in gram per 100 m counted on transects against normalized difference vegetation index (NDVI) values. Predicted values of GAMM are shown as red line, twice standard error as dashed lines.

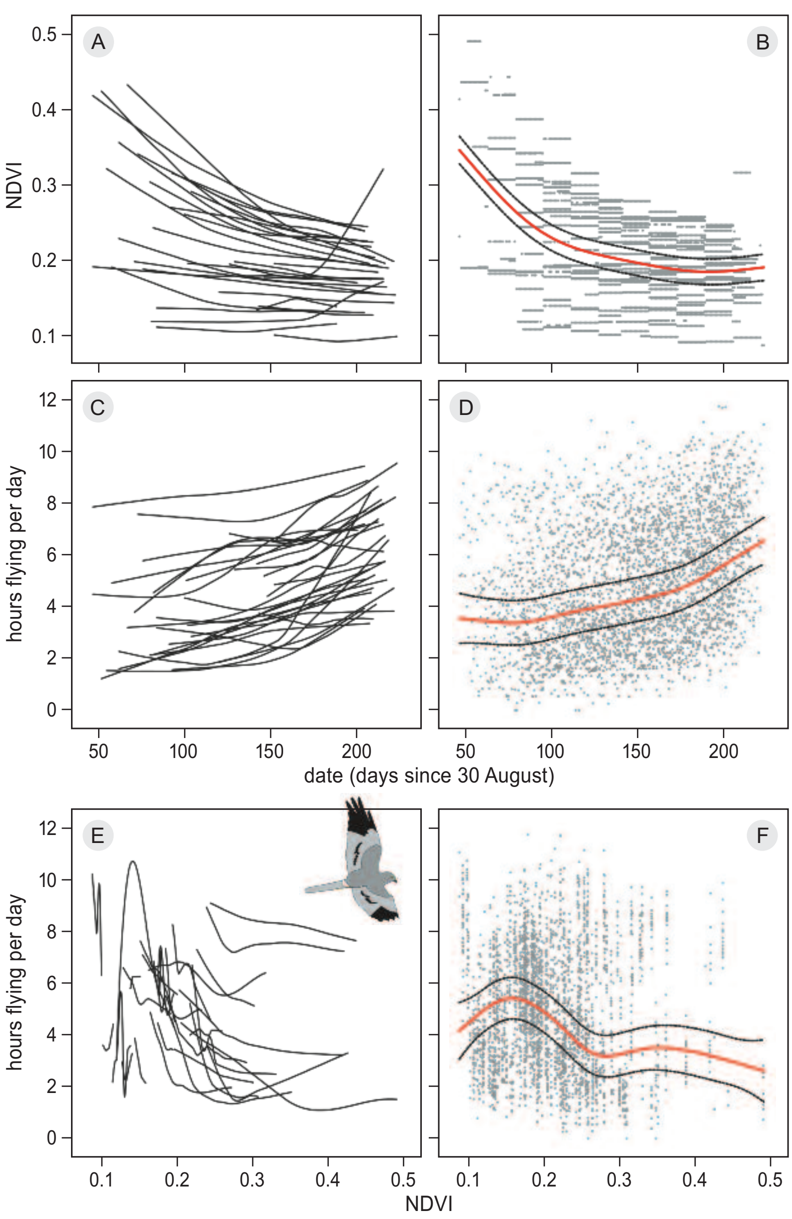

Figure 3.4. Seasonal changes in (**A/B**) NDVI experienced by 31 GPS-tracked Montagu's Harriers at their final wintering site. (**C/D**) Daily hours spent flying of GPS-tracked Montagu's Harriers at their final wintering site. (**E/F**) Daily time spent flying of Montagu's Harriers in relation to normalized difference vegetation index (NDVI) used as proxy for grasshopper abundance. Lines are loess smoothed raw data per individual on the left (A,C,E) and raw data overlayed by predicted values of GAMMs (red) and two times standard errors (dashed lines) on the right (B,D,F).

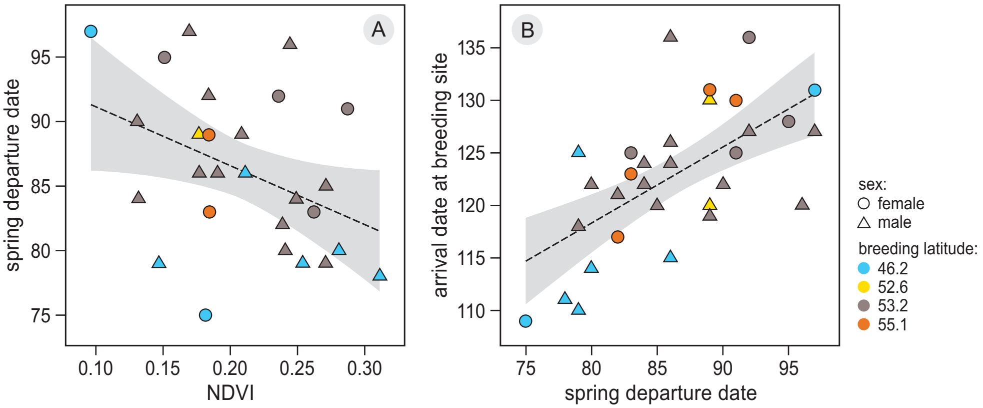

Figure 3.5. (**A**) Departure date (days since 1 January) of Montagu's Harriers for spring migration in relation to mean NDVI values at their final wintering site. (**B**) Arrival date at the breeding area in relation to spring departure date from the last wintering area. Breeding latitude of individuals is indicated in different colours (blue: France, yellow: Germany, black: Netherlands, red: Denmark), sex with different symbols. Linear model is indicated by black line. For statistics see Table 1I,J.

Discussion

In this study, we first describe the seasonal deterioration of environmental conditions at the final wintering sites of Montagu's Harriers wintering in the Sahel. Secondly, we show that deteriorating conditions (i.e. drying out of the landscape) are associated with a decline in grasshopper abundance; the harriers' main prey during winter. Thirdly, we reveal that harriers respond to these changes in environmental conditions by increasing their daily flight time, distance and home range size during their stay at the last wintering site. Finally, our findings indicate that unfavourable conditions at the final wintering site could have carry-over effects to later annual cycle stages and that in dry years the deterioration of environmental conditions might have fitness consequences by showing that birds in drier areas forage more intensively, depart later on spring migration and arrive later at their breeding grounds.

Why do harriers increase foraging time?

Previous work on satellite tagged Montagu's Harriers revealed that individuals visit several wintering sites during the season following a southwards shifting 'green belt' of vegetation and thereby stay within the range of NDVI values containing most grasshoppers (Trierweiler *et al.* 2013). In West Africa, this southward shift comes to an end at the southern border of the Sahel, and we show that at those final wintering sites, birds still do experience declining densities of grasshoppers during their stay.

The GPS-tracked Montagu's Harriers increased their daily flight time, distance covered and area used during the stay at their final wintering site. Individual variation in those behavioural measures was enormous, with individuals spending on average from 2.2 up to 8.4 h flying per day. Whether this variation resulted from variation between wintering sites or heterogeneity in individual quality could not be assessed in our study since our data set contained only one bird per area, covering the whole wintering range of the north-western breeding populations between Senegal and Niger (Limiñana *et al.* 2012c; Trierweiler *et al.* 2013). We also have no information on the number of conspecifics and the number of other acridivorous species, and thereby the within- and between-species competition in the areas of our GPS-tracked individuals, that may further explain variation.

Additionally, the observed behavioural changes may also be explained by preparation for spring migration. Many migrants do store large fuel loads prior to crossing ecological barriers, such as the Sahara, and these stores are gained during the last weeks before departure (Newton 2008). After departing from their last wintering site, Montagu's Harriers head straight north crossing the Sahara desert (cf. Fig. S2) and normally just stopover in North Africa (Trierweiler *et al.* 2014). However, if the increased flight time over the season was solely to store reserves for migration, we would have expected a stronger increase prior to departure rather than a more gradual increase over 3 months, as birds generally have a high capacity of accumulating fat reserves, at least when foraging conditions are favourable (Kvist & Lindström 2003). In addition, Montagu's Harriers migrate to a large extent by soaring flight (Limiñana *et al.* 2013), a relatively energy-efficient flight mode (Hedenström 1993), and are fly-and-forage migrants (Trierweiler 2010), which might further reduce the need to store huge fuel loads, assuming that harriers can find food during the Sahara crossing. We thus conclude that Montagu's Harriers alter their behaviour in response to deteriorating conditions in the Sahel.

Moreau's Paradox

Moreau wondered in 1972 how millions of Palaearctic migrants could winter in the dry Sahel and prepare for spring migration in what seem to be continually deteriorating conditions (Moreau 1972). We discuss three possible ways in which Moreau's Paradox might be resolved.

First, the paradox can be resolved because the assumption of deteriorating food abundance in the course of the dry season is false. This is clearly not the case for Montagu's Harriers (cf. Fig. 3.2) and other acridivorous species in Senegal. However, it might be true for other areas or other species relying on different food sources. Even though our transect counts covered only wintering areas at the western most range of the wintering distribution of Montagu's Harriers, the similar relationship reported by Trierweiler *et al.* 2013 for Niger and the importance of grasshoppers as prey found in pellets in other areas (Trierweiler & Koks 2009; own unpublished data) make us confident to believe that this is a common pattern. Morel (1973) argued that migrants arrive in the Sahel just at the end of the rainy season when vegetation is rank and invertebrates numerous. During their stay, at least some trees continue to have leaves, flowers and fruit production. Writing mainly about passerines, he further argued that potential competition with local species might be low since these often perform within-African movements (Morel 1973). Within the West African Sahel, Zwarts *et al.* (2015) recently found the highest numbers of insectivorous woodland bird migrants in the driest and most desiccated parts. They further suggested that migrant Palaearctic birds prefer thorny tree species (e.g. *Acacia* and *Balanites*) that are richer in arthropods. However, it is likely that insect densities on these trees also decline during the dry season, and birds still need to prepare for migration during the worst period of the season. Field data on prey availability and diet choice for insectivorous tree dwelling birds in space and time are still lacking, and hence, we cannot come to a general conclusion.

A second solution to the paradox may be that prey abundance is decreasing, but birds switch to alternative prey. Currently we have no indication that this occurs in wintering Montagu's Harriers, despite the fact that prey switching certainly occurs in breeding populations. Indeed, breeding Montagu's Harriers can forage on a wide range of prey, with small birds being their main prey in many areas, whereas voles dominate in other areas (Terraube & Arroyo 2011). In populations that depend strongly on Common Voles *Microtus arvali*s, harriers switch to alternative prey like songbirds, reptiles and large insects in years with low vole densities (Millon *et al.* 2002; Koks *et al.* 2007). In winter, the species is highly acridivorous (Mullié 2009; Trierweiler & Koks 2009; Mullié & Guèye 2010; Trierweiler *et al.* 2013), and our pellet samples from Senegal in 2014 show no obvious switch in diet between the middle and the end of the wintering period (own unpublished data). But in other wintering areas, such as Niger, fewer grasshoppers (<60%) are found in pellets (Trierweiler & Koks 2009), and hence, diet switches may be part of the solution in some ecological conditions. Diet switches might occur in other Sahelian migrants, since some songbirds can switch to berries (e.g. berries of *Salvadora persica*: Morel 1973; Zwarts *et al.* 2015) or nectar (Salewski *et al.* 2006).

Thirdly, prey abundance may be decreasing but birds cope with this by adapting their foraging behaviour. This is what we found for Montagu's Harriers which increased their flight time with decreasing prey abundance. However, in dry areas or years, this seems to come at the cost of a late departure that might subsequently carry over to later annual cycle stages (Norris & Marra 2007).

Ultimate effects

Local ecological conditions at the end of the winter affect individuals, as we show that harriers wintering in areas with less vegetation and hence lower food abundance departed later in spring (Fig. 3.5), suggesting a link between food availability and individual condition. Departure date might be strongly influenced by individual annual schedules with birds breeding at more southern latitudes departing earlier and consequently being able to winter in more northern and drier areas, as shown for Pied Flycatchers *Ficedula hypoleuca* (Ouwehand *et al.* 2016). Still, the effect of NDVI on departure date of our harriers remained significant when testing for effects of latitude of wintering and breeding site, as well as sex. In a completely different ecosystem, American Redstarts *Setophaga ruticilla* that winter in habitats with higher food abundance do depart earlier than individuals in low-quality habitats at the same site, and departure is earlier in years with more rainfall (Studds & Marra 2011). For the Sahel system, there is evidence showing that annual mean spring migration time through the Mediterranean is later after dry winters (Both 2010; but see Robson & Barriocanal 2011 for opposite trends), as is spring arrival at breeding sites (Saino *et al.* 2004; Both *et al.* 2006;

Gordo & Sanz 2008; Balbontín *et al.* 2009; Tøttrup *et al.* 2012a). As timing affects later fitness consequences in most migratory species, Moreau rightly drew attention to the difficulty migrants might have when leaving their wintering grounds during the worst ecological circumstances in the season. Low Sahel rainfall has also been shown to lower overwinter survival in Palaearctic migrant species that spend the winter here (Den Held 1981; Peach, Baillie & Underhill 1991; Zwarts *et al.* 2009), which could be mostly happening through conditions at the end of the winter period hampering preparation for spring migration. Indeed, mortality in Montagu's Harriers is highest during the spring crossing of the Sahara desert (Klaassen *et al.* 2014). The same is not only also true for other migrants, but even more pronounced in drier years (Zwarts *et al.* 2009). We should stress that our data are biased towards individuals that successfully returned to the breeding areas; thus we cannot infer mortality. The later departure from the driest wintering sites could suggest that other individuals departed in too low condition to successfully migrate to the breeding areas and were never seen again. Alves *et al.* (2012) showed for Icelandic Black-tailed Godwits *Limosa limosa islandica* that individuals in poor condition did not migrate. Late departure can be associated with late arrival at the breeding sites (cf. Fig. 3.5B; Jahn *et al.* 2013; Lemke *et al.* 2013), and late arriving individuals often have lower reproductive success (Kokko 1999; Smith & Moore 2004). Additionally, it has been shown for several species that breeding performance is indeed lower in years that followed a drier winter (Zwarts *et al.* 2009, p. 472ff and references therein). We thus suggest that wintering in habitats with low food availability before the onset of spring migration may negatively affect fitness. Thus, especially extremely dry years (as during the severe droughts in the 1970s and 1980s) might strongly influence survival and subsequent breeding success. Ongoing climate change with possibly less rainfall in the Sahel region paired with increased human pressure on natural and agricultural habitats resulting in degradation and desertification might make this late wintering period prior to migration more demanding, likely affecting overall population size. For a species that is depending on immense protection efforts in Europe, this might have disastrous effects and we need to investigate small-scale habitat use in wintering areas to gain knowledge that could be used to improve the year-round conservation of the species by means of habitat conservation and management along the flyway.

Acknowledgements

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Popping-Fonds, Dobberke Stichting, Deutsche Ornithologen Gesellschaft, Huib Kluijverfonds, KNAW Fonds Ecologie, Triodos Fonds and Prins Bernhard Cultuur Fonds. We thank J. Gill, L. Zwarts, H. Mallion and an anonymous reviewer for valuable comments on an earlier draft of this manuscript. L. Zwarts kindly provided us the data set on annual rainfall at Kaolack.

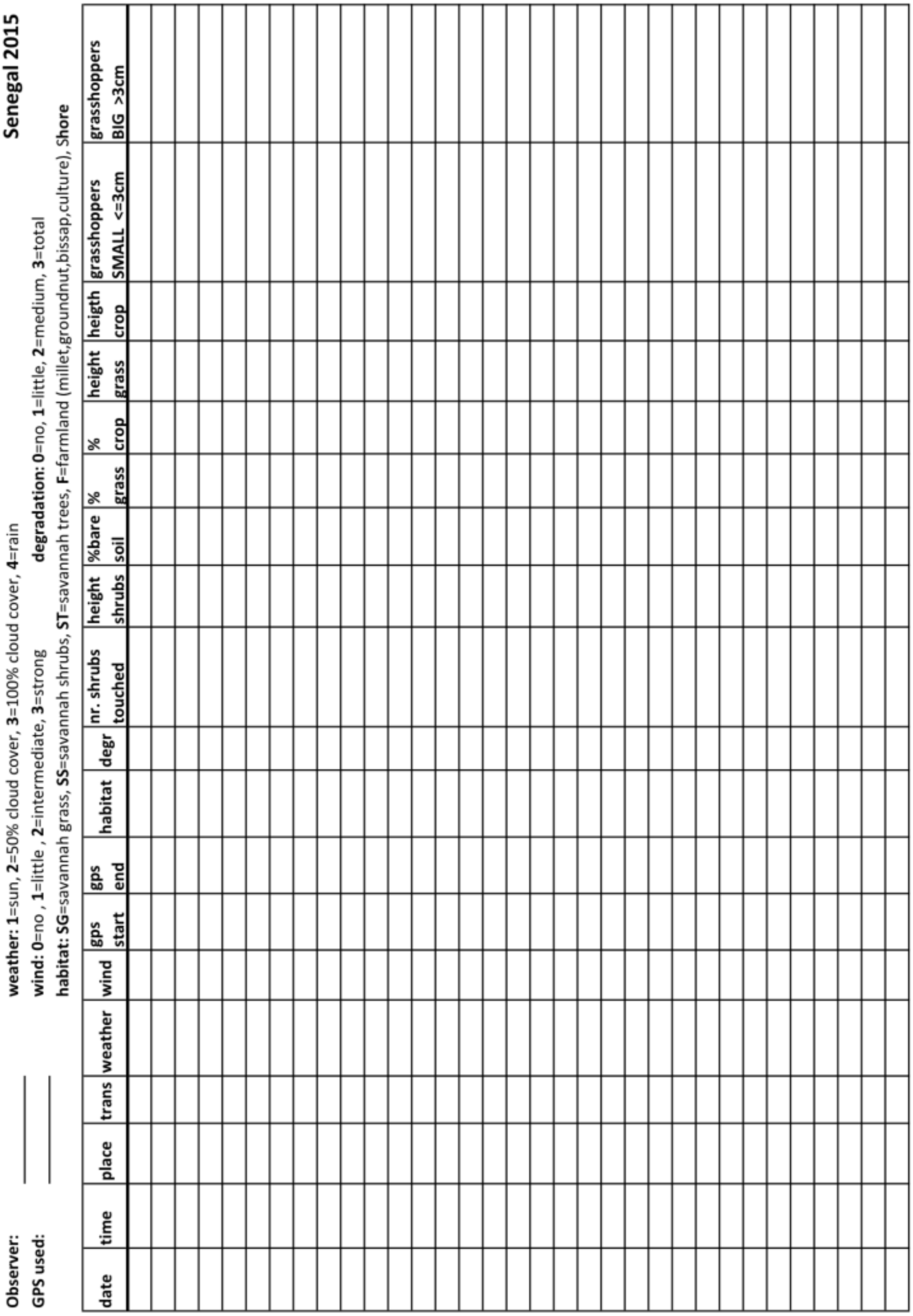
Data accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.144sv

Supporting information

Appendix S1

Grasshopper transect count form used for sampling in Senegal in 2014 and 2015.



Senegal 2015

Observer: ____________

GPS used: ____________

weather: 1=sun, **2**=50% cloud cover, **3**=100% cloud cover, **4**=rain

wind: 0=no , **1**=little , **2**=intermediate, **3**=strong **degradation: 0**=no, **1**=little, **2**=medium, **3**=total

habitat: SG=savannah grass, **SS**=savannah shrubs, **ST**=savannah trees, **F**=farmland (millet,groundnut,bissap,culture), **Shore**

date	time	place	trans	weather	wind	gps start	gps end	habitat	degr	nr. shrubs touched	height shrubs	%bare soil	% grass	% crop	height grass	heigth crop	grasshoppers SMALL <=3cm	grasshoppers BIG >3cm

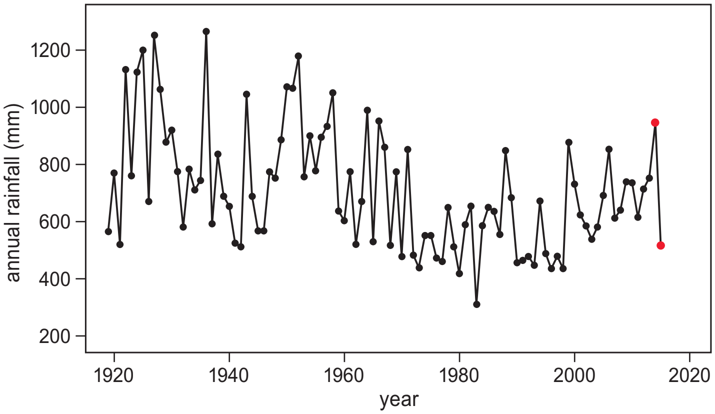


Figure S1. Annual rainfall (mm) at Kaolack, Senegal (14.15°N 16.08°W). Data kindly provided by L. Zwarts. The years 2014 and 2015, during which the study took place, are indicated with red dots.

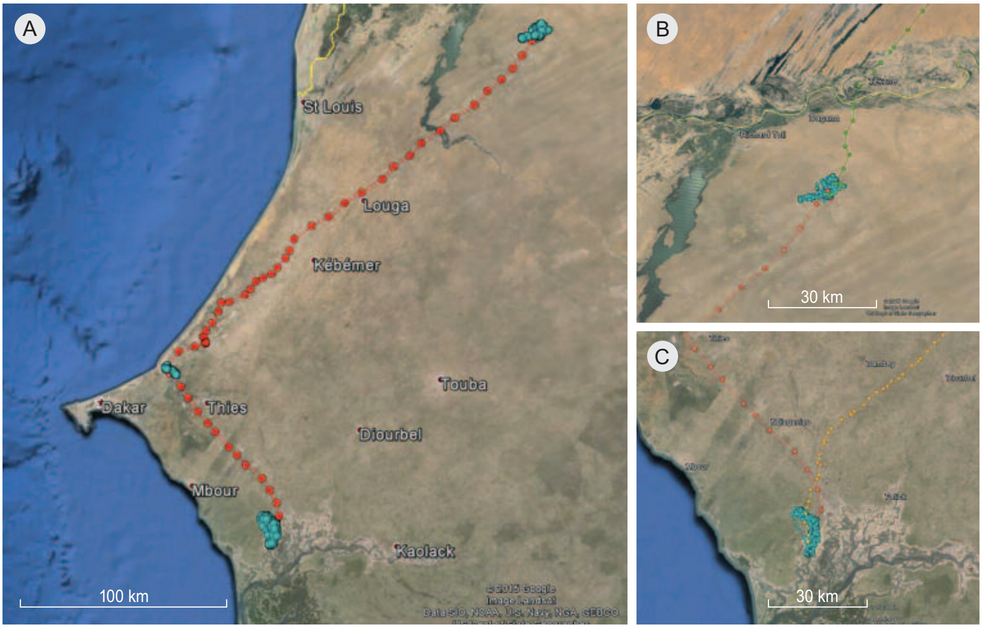


Figure S2. Example of a typical winter season of a male Montagu's Harrier wintering in Senegal. (**A**) The consecutive wintering sites (light blue) with travel days between sites (red) of male Edwin in winter 2013/2014. (**B**) Arrival day (green) to first site on 17.09.2013. (**C**) Departure day (yellow) on 27.03.2014, clearly distinguishable from stay at site three (light blue).

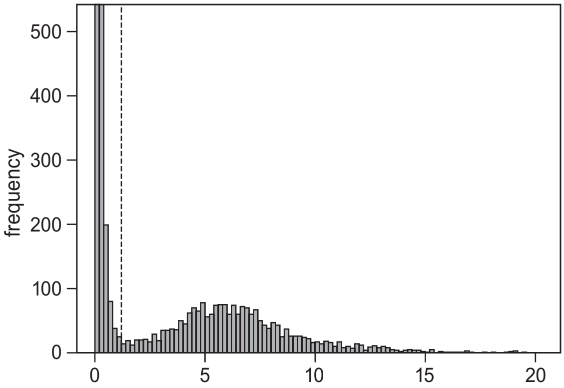


Figure S3. Example of a frequency distribution of instantaneous flight speeds (in m s^{-1}). A threshold of 1.2 m s^{-1} was used to distinguish between flying and sitting (dashed vertical line).

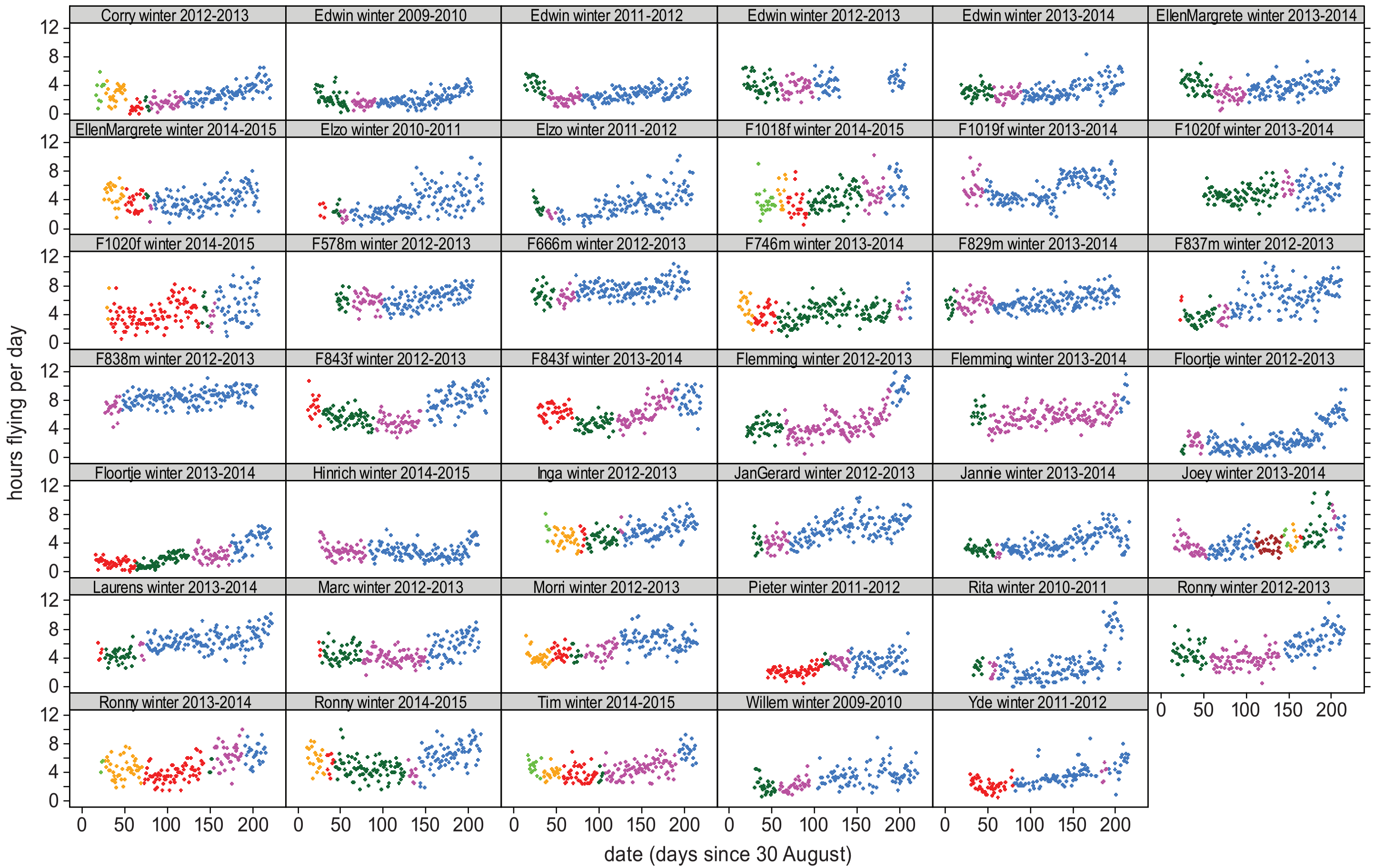


Figure S4. Daily hours spent flying of GPS-tracked Montagu's Harriers during the whole wintering season. Different colours indicate different wintering sites, the final site is shown in blue.

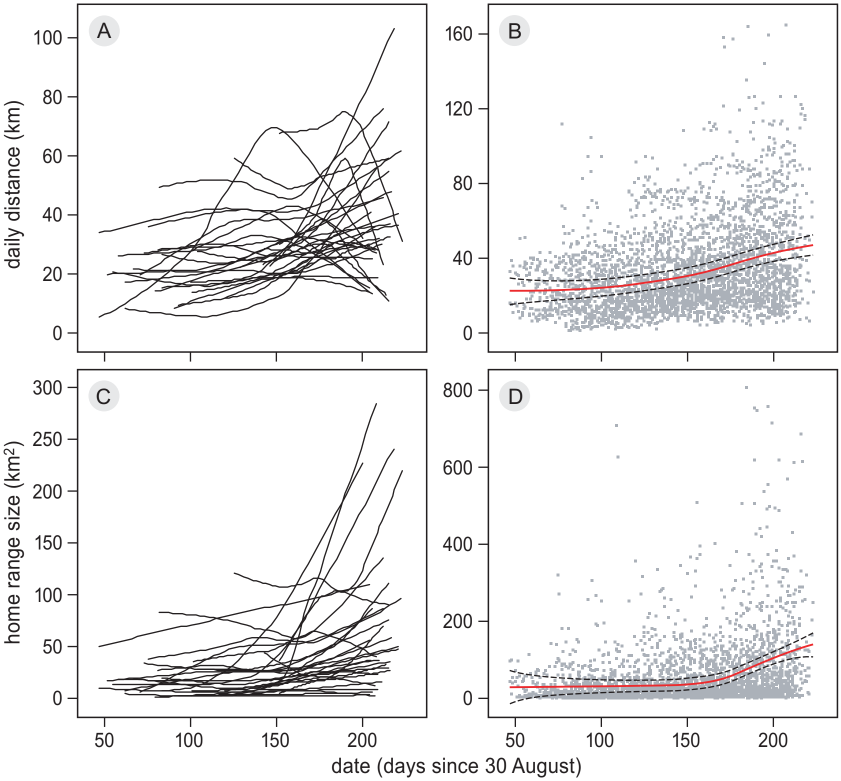


Figure S5. (**A/B**) Cumulative distance of GPS-tracked Montagu's Harriers at their final wintering site. (**C/D**) Kernel home range size (95%) of GPS-tracked Montagu's Harriers at their final wintering site. Given are loess smoothed raw data per individual on the left and raw data overlaid by predicted values of GAMMs (red) with two times standard errors (dashed lines) on the right. Scales differ between left and right panels. Due to scaling, 8 and 7 points are not shown on the right on top and bottom, respectively.

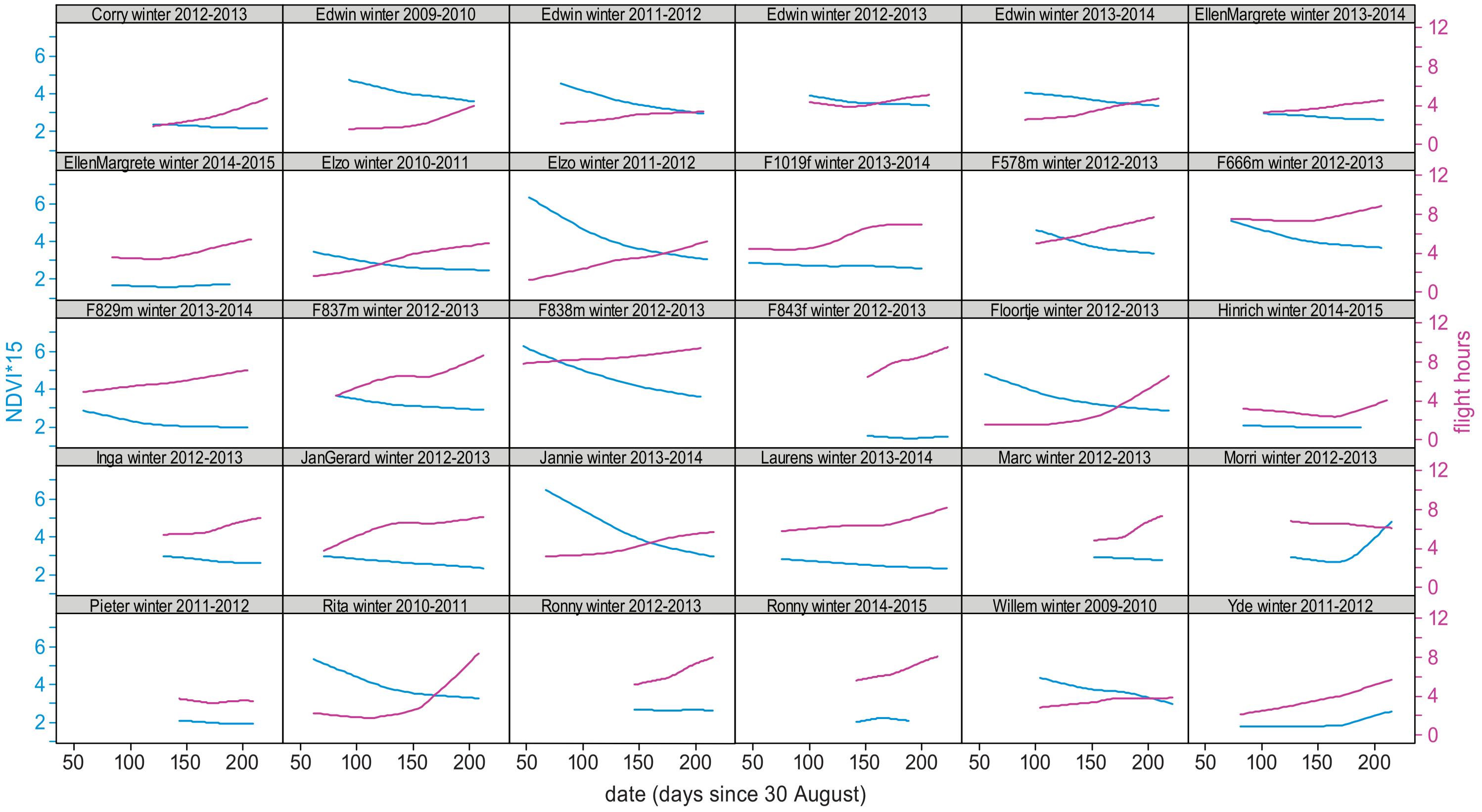


Figure S6. Daily time spent flying (pink, right axis) and Normalized Difference Vegetation Index (NDVI)*15 (blue, left axis) used as proxy for grasshopper abundance at the final wintering site of Montagu's Harriers. Lines show loess smoothed raw data.

4

Rare case of an adult male Montagu's Harrier *Circus pygargus* over-summering in West Africa, as revealed by GPS-tracking

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Abstract

Over-summering within or near the African wintering range by immature, non-breeding individuals occurs regularly in several species of long-distance migratory raptors, yet the extent of over-summering in Africa by adult birds remains unclear. In this study, we describe a case of an adult Montagu's Harrier over-summering in Africa, as revealed by GPS-tracking. By relating detailed knowledge of the bird's movements to remotely sensed environmental data (normalized difference vegetation index, NDVI), we show that over-summering in this case was likely related to an exceptionally difficult breeding season the previous year rather than an effect of adverse weather conditions encountered during the winter or a failed attempt to migrate. Various factors are discussed as potential driving forces behind the bird's intra-African movements. Finally, we relate the documented case to a large number of North European Montagu's Harriers studied by telemetry and show that over-summering in Africa by adult individuals is indeed a rare event.

Introduction

Migratory routes connect European breeding sites with non-breeding sites in Africa through the movement of more than two billion birds each year (Webster *et al.* 2002; Hahn *et al.* 2009). Migration allows birds to exploit northern seasonal resources during the breeding season, and it is a very common behaviour in terms of both number of bird families and total number of individuals involved (Newton 2010). However, not all individual migrants return to the breeding grounds in spring, as some may defer migration and remain in Africa during the European summer. Such over-summering has been reported mainly for non-breeding subadult birds of large and long-lived species, including several species of migratory raptors (e.g. Österlöf 1977; Gschweng *et al.* 2008; Mellone *et al.* 2011). Over-summering also occasionally occurs in adult raptors (Thiollay 1989; Fransson 2001), yet to our knowledge, detailed information on individual cases is lacking in the scientific literature.

Several ideas have been put forward to explain why individuals remain at or near their winter quarters in Africa during the breeding season. Migration entails a high mortality risk (Klaassen *et al.* 2014), and by deferring migration, subadult non-breeding birds may generally increase their chances of survival until sexual maturity is reached (Newton 2010). However, reasons for adult breeding birds staying the summer in Africa are probably specific to each individual. Poor body condition, whether due to difficult conditions in Africa or a consequence of an exhaustive breeding effort the previous year, might impede spring migration. The same is true for exceptionally harsh weather conditions. In order to understand the causes leading to over-summering by adult birds, detailed information on individual movements and behaviour is needed, ideally in combination with information on relevant environmental conditions.

Recent developments in tracking techniques have greatly improved our knowledge of the movement patterns of individual raptors (Catry *et al.* 2011; García-Ripollés *et al.* 2010; Klaassen *et al.* 2014), and Montagu's Harriers *Circus pygargus* have been tracked intensively to study the species' migration system (Limiñana *et al.* 2007; Trierweiler *et al.* 2007; Klaassen *et al.* 2014; Trierweiler *et al.* 2014) and wintering ecology (Limiñana *et al.* 2012a; Trierweiler *et al.* 2013; Schlaich *et al.* 2016). Furthermore, ecologists have found ways to combine field-based studies with remote sensing data, and since such large-scale data sets are now easily accessible, they are widely used in ecological research (Kerr & Ostrovsky 2003). Trierweiler *et al.* (2013) used remote sensing data on the normalized difference vegetation index (NDVI) to show that Montagu's Harriers track a high abundance of resident grasshoppers, the harriers' main prey in winter, by gradually moving southwards during the winter period.

Here we report an unprecedented case of over-summering in an adult male Montagu's Harrier tracked from its breeding location in Denmark. The bird spent a year and a half in West Africa, during which time it visited several different sites. These intra-African movements are described in detail and related to concurrent environmental conditions, leading to a discussion of the driving forces behind the harrier's over-summering behaviour and whether it attempted to migrate to Europe in spring but failed to do so or deliberately stayed in Africa.

Methods

We studied a small breeding population of Montagu's Harriers in Denmark, currently consisting of 20–30 pairs. This population breeds at the northwestern limit of the species' breeding range and forms part of the North European meta-population (see Trierweiler *et al.* 2014). The Montagu's Harrier is categorized as endangered on the Danish Red List of threatened species (Wind & Pihl 2004), and breeding pairs have been monitored closely for two decades through a national conservation and research programme run by DOF-BirdLife Denmark (Rasmussen *et al.* 2015). Between 2011 and 2014, nine adult Montagu's Harriers were fitted with UvA-BiTS GPS trackers to study the birds' space use and habitat choice, ultimately to optimize local conservation efforts. UvA-BiTS (University of Amsterdam Bird Tracking System) is a flexible GPS-tracking system with two-way interaction between the GPS trackers and a local antenna system (Bouten *et al.* 2013). Data is downloaded remotely when a tracker is within range of a local antenna system and otherwise stored on the device until it connects again. This means that no information on the position of a tracked bird can be retrieved until it returns to the study area. Consequently, birds can be overlooked if dispersing to other areas.

In July 2011, an adult male Montagu's Harrier was caught near its nest in Ballum, southwest Denmark, and fitted with an UvA-BiTS GPS tracker. This individual, named "Jeppe" (GPS tracker ID #583), had been ringed as a nestling in the same area in July 2008, so upon recapture it was in its fourth calendar year. During the breeding season of 2011, Jeppe bred successfully, raising three chicks. In 2012, Jeppe was not observed in the breeding area and was presumed dead or breeding elsewhere. In May 2013, it returned to the study area to breed, and the GPS data spanning the period between September 2011 and May 2013 were downloaded. From September 2011 to February 2013, the tracker had recorded GPS positions every 30 min during the day and once per hour during the night. From 11 February 2013, when the memory of the tracker was nearly full, the position frequency decreased to one position every 6 h. Hence, from 11 February 2013 Jeppe's movements were recorded at a lower resolution. Jeppe's breeding attempt in 2013 was unsuccessful and the bird has not been observed since.

GPS data on Jeppe's movements were processed in R 3.1.2 (R Core Team 2014). Positions with trajectory speeds (speed between two subsequent GPS fixes) higher than 25 m s^{-1} were regarded as outliers and removed from the data set. Positions with altitudes higher than 5 km and instantaneous speeds higher than 25 m s^{-1} (both as measured by the GPS) were also discarded. Arrival and departure dates at different sites were determined manually using Google Earth (https://earth.google.com/). Maps were produced using the package *RGoogleMaps* version 1.2.0.6 (Loecher & Ropkins 2015). In order to investigate whether the timing of Jeppe's movements coincided with the timing of regular migratory movements, we inspected migratory movements of eight additional male Montagu's Harriers from Denmark (n = 1) and the Netherlands (n = 7) tracked using UvA-BiTS GPS trackers between 2011 and 2013.

To investigate the environmental conditions encountered by Jeppe during its stay in Africa, we looked at Moderate-resolution Imaging Spectroradiometer (MODIS) NDVI data, which provides a remotely sensed measure of the level of greenness and is available at high spatial and temporal resolution. Trierweiler *et al.* (2013) and Schlaich *et al.* (2016) used NDVI as a proxy for grasshopper abundance in Sahelian wintering sites (with grasshopper densities peaking at intermediate NDVI values). Here we do not use NDVI as a proxy for grasshopper density per se, but rather as an indication for the general ecological conditions Jeppe experienced at the different sites, assuming that conditions are unfavourable at very low NDVI values (Tøttrup *et al.* 2012a; Thorup *et al.* 2017). This approach was adopted because Jeppe covered a larger geographical range than the Sahel, including tropical woody savannah (see Results), and a larger temporal window of the year, for which we have no information on grasshopper densities and thus do not know the relationship between grasshopper abundance and NDVI. We used the R-package *MODISTools* (version 0.94.6, Tuck *et al.* 2014) to download NDVI data for a 1.25 × 1.25 km area (i.e. a 5 × 5 array of 250 × 250 m pixels) centred at each site visited by Jeppe to reconstruct the conditions the bird had experienced during the study period. In addition, we downloaded NDVI data for Jeppe's main "regular" wintering site for a range of years (2001–2014), in order to inspect whether the site was exceptionally dry during the winter of 2011/2012.

Results

Route

In May 2013, the male Montagu's Harrier Jeppe returned to its Danish breeding grounds after having spent more than 17 months in West Africa. During the winter of 2011/2012, the harrier used three different wintering sites in Mauritania and Senegal (sites A, B and C, see Fig. 4.1, Table 4.1). Instead of departing north from its main wintering site (C), Jeppe moved more than 200 km south in March 2012 at the onset of other male harriers' northbound spring migration (Fig. 4.2). After spending more than a month in Guinea-Bissau (sites D and E), the bird moved almost 600 km north and then roamed a large area in the central part of southern Mauritania (sites F and G) from May to July 2012. During July, in the middle of the European breeding season, Jeppe moved even further north to the northern edge of the Sahel (sites H and I). The bird remained four months at site I, where it also stayed during the autumn migration period of the other harriers (Fig. 4.2). During the remaining part of the following winter, Jeppe used four different sites (J, K, A and G). Site A was the only site visited in both winters, yet one of the sites used during the summer (site G, Fig. 4.1) was also revisited. Jeppe departed from site G on spring migration on 17 March 2013 and arrived at the breeding site in Denmark on 29 April 2013, with speed and timing comparable to other tracked harriers (Fig. 4.2).

Environmental conditions

NDVI values for Jeppe's main wintering site (site C) in 2011/2012 did not differ markedly from other years' values (Fig. 4.3). This is true for the summer peak as well as for the level during the winter period. These NDVI values suggest that precipitation at site C reached average levels during the summer of 2011, and that site C was not exceptionally dry during the time Jeppe visited the area during the winter of 2011/2012.

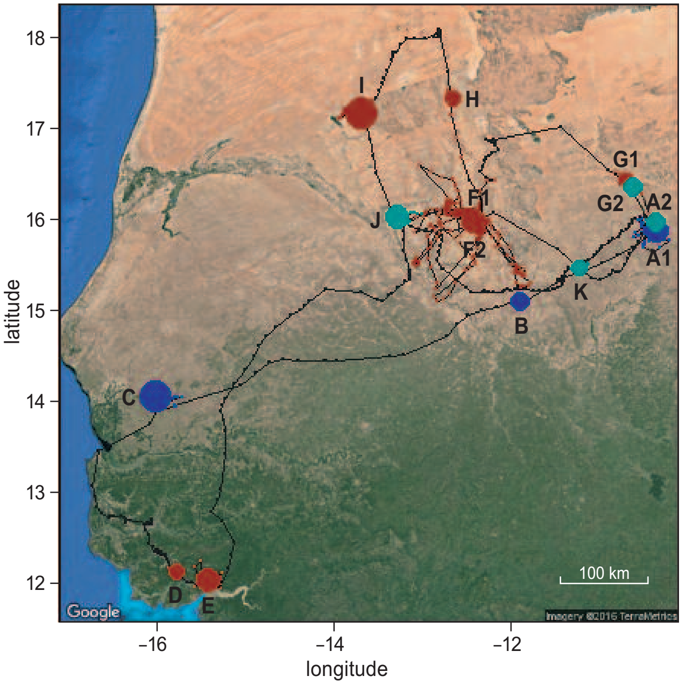

Figure 4.1. Map of Jeppe's movements during its 17 months in West Africa from October 2011 to March 2013. Wintering sites 2011/2012 are *dark blue*, summering sites 2012 are *red*, and wintering sites 2012/ 2013 are *light blue*. Symbol size is proportional to length of stay. Smaller dots connected by the *black* line represent GPS positions.

Table 4.1. Overview of Jeppe's arrival and departure dates to and from sites visited during the 17 months in Africa.

Site	Country	Arrival	Departure
A	Mauritania	07.10.2011	10.11.2011
B	Mauritania	10.11.2011	24.11.2011
C	Senegal	25.11.2011	18.03.2012
D	Guinea-Bissau	23.03.2012	28.03.2012
E	Guinea-Bissau	29.03.2012	04.05.2012
F	Mauritania	06.05.2012	09.05.2012
G	Mauritania	10.05.2012	16.05.2012
F	Mauritania	17.05.2012	02.07.2012
H	Mauritania	02.07.2012	06.07.2012
I	Mauritania	08.07.2012	17.11.2012
J	Mauritania	17.11.2012	28.01.2013
K	Mauritania	31.01.2013	07.02.2013
A	Mauritania	09.02.2013	27.02.2013
G	Mauritania	27.02.2013	17.03.2013

The NDVI values Jeppe encountered during its 17 months' stay in Africa varied considerably both in space and over time (Fig. 4.4). During the first winter (2011/2012), Jeppe left a particular site each time NDVI dropped to a baseline level of around 0.2. As a consequence of moving southward, the bird repeatedly encountered new green areas. By the southward movement from site C to sites D and E, Jeppe moved into tropical woody savannah habitat with notably higher NDVI values (note that these sites are much greener year-round compared to sites in the Sahel). Jeppe returned to the Sahel (sites F and G) prior to the onset of the rainy season, while NDVI was still at a very low level - even lower than the baseline level that apparently induced Jeppe's movements during the winter. These were the driest circumstances Jeppe experienced during the over-summering period. In July 2012, Jeppe moved further north to areas that are even drier during the dry season (sites H and I). Jeppe arrived here during or just before the rainy season, remained at site I throughout the NDVI peak, and did not leave the site until NDVI had dropped again to the baseline level

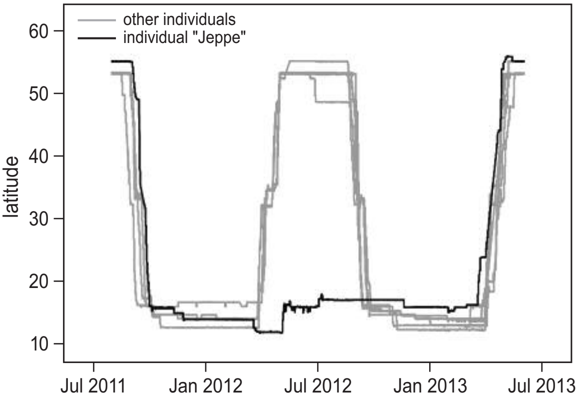

Figure 4.2. Latitudinal movements of nine male Montagu's Harriers fitted with GPS trackers between 2011 and 2013. Two males were breeding in Denmark; all others were breeding in the Netherlands.

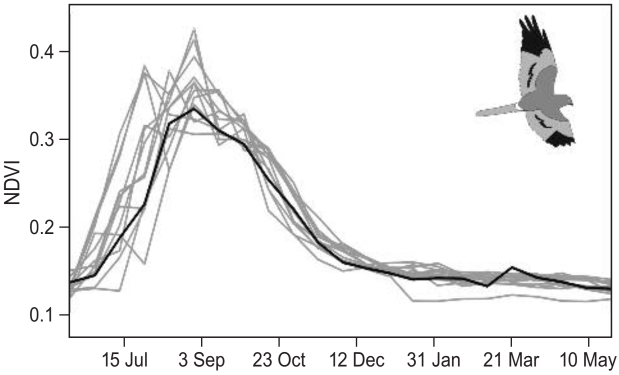

Figure 4.3. Annual variation in NDVI for site C, the main wintering site of Jeppe, from June 2001 through to June 2014. Values from June 2011 to June 2012 are shown in *black*.

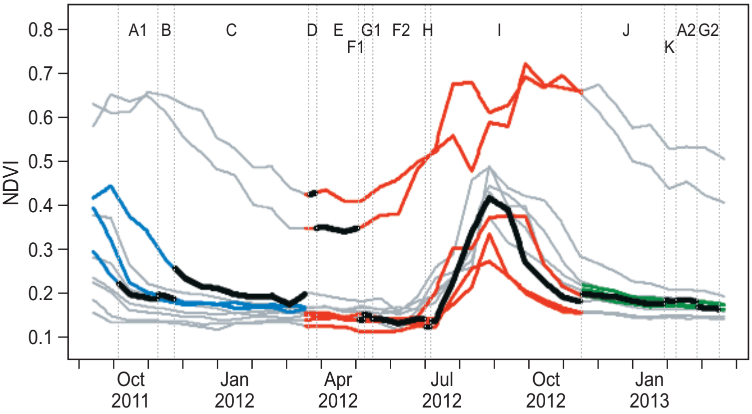

Figure 4.4. NDVI values recorded at all sites visited by Jeppe throughout his stay in Africa, with thick *black* lines indicating values experienced by Jeppe during the time it stayed at each site. *Blue* lines indicate sites visited during the winter 2011/2012, *red* lines indicate summering sites, and *green* lines indicate sites visited during the winter 2012/2013.

(November 2012). During the remaining part of the winter, Jeppe again moved from site to site (J, K, A and G). Particularly notable is the movement from site A to G in February 2013, as this brought Jeppe to a site that had lower NDVI values than the previous one.

Discussion

This study reveals the first documented case of over-summering in Africa by an adult Montagu's Harrier. GPS tracking provided detailed knowledge of the bird's movements, which we here relate to season and NDVI values. We found no evidence that this case of over-summering was caused by unusual weather events or patterns of precipitation, and the bird's behaviour showed no indications of it being injured or trapped at any point. In fact, the bird visited a notably large number of sites during its 17 months in West Africa.

Over-summering in Africa by adult Montagu's Harriers is rare, which is emphasised by the fact that the current case constitutes the only example among 90 individuals tracked over 129 winters by either satellite telemetry (n = 54 individuals over 72 winters, own data 2005-2016; Trierweiler *et al.* 2014) or GPS trackers (n = 36 individuals over 57 winters, own data 2009-2016; Vansteelant *et al.* 2015; Schlaich *et al.* 2016).

Reasons for staying in Africa

Local weather conditions have been shown to affect bird migration in various ways (e.g. Strandberg *et al.* 2008; Tøttrup *et al.* 2012a; Vansteelant *et al.* 2015), and it is indeed possible that unfavourable weather conditions during spring migration impeded Jeppe's departure. However, when faced with unfavourable weather conditions in spring, Marsh Harriers *Circus aeruginosus* tracked by satellite telemetry always made several attempts to cross the Sahara, and although some of these harriers eventually aborted the desert crossing and retreated to staging sites in the Sahel, initial movements were always directed northwards and clearly revealing intentions to migrate (Strandberg *et al.* 2008). Quite the opposite was seen here, since Jeppe moved further south during the usual spring migration period and did not make any northward movements from its final wintering site in March 2012. Hence, it is unlikely that the over-summering by Jeppe was induced by a failed attempt to migrate due to unfavourable weather conditions at the onset of spring migration.

An alternative explanation is that the conditions experienced by the bird during the preceding winter were generally unfavourable, entailing a poor body condition and thus impeding migration. This may have led Jeppe to explore foraging opportunities further south, attempting to improve its body condition prior to migrating. In terms of NDVI, conditions at the main wintering site during the winter of 2011/2012 were very similar to other winters (Fig. 4.3), thus we do not assume that the bird experienced particularly harsh environmental conditions during the winter preceding its over-summering. However, other factors may have resulted in low food availability or in other ways caused suboptimal living conditions.

Finally, the remarkable over-summering behaviour of Jeppe could be the result of an exhaustive breeding effort the previous year. It has been suggested that late breeding might result in an increased mortality risk during autumn migration in Montagu's Harriers, since late breeders have less time to prepare for migration (Limiñana *et al.* 2012c). Furthermore, breeding is a truly demanding life history stage in raptors and may cause significant post-breeding mortality (Daan *et al.* 1996; Klaassen *et al.* 2014). The breeding season of 2011 was certainly very demanding for the Danish Montagu's Harriers. The summer was characterized by unusually high levels of precipitation, and monthly rainfall during June through to August was 71 % above average (DMI 2011). Breeding success was below average as only 15 fledglings were produced by 25 pairs (Rasmussen & Clausen 2011), yet Jeppe managed to raise three young (one fifth of the Danish chicks in 2011; only six pairs bred successfully). It is conceivable that this effort somehow forced him to remain the subsequent summer in Africa and thereby defer breeding in 2012. Lending some support to this is the fact that the female Jeppe was paired with in 2011 (a female tracked by satellite telemetry from 2009 to 2014) arrived very late at the breeding grounds and did not attempt to breed in 2012 (own data).

Drivers of intra-African movements

In spring 2012, Jeppe left its main wintering site at the usual time of spring migration. Although this spring movement might be interpreted as migratory restlessness (Gwinner 1996), Jeppe remained at site I and did not express any restlessness during the entire period of autumn migration in 2012. Thus, its movements during spring and early summer 2012 may have been determined by other factors.

Jeppe used a notably large number of sites in West Africa during the summer of 2012, each move conceivably driven by prevailing environmental conditions. In the Sahel region, man-made habitat changes have amplified negative impacts of droughts and climate change (Zwarts *et al.* 2009), and it may be difficult for a harrier to survive here during late spring, as environmental conditions gradually deteriorate until the onset of the summer rains. Jeppe's southward move into tropical woodland savannah in March 2012 thus appears sensible.

However, tropical woodland savannah is not a typical habitat for Montagu's Harriers, and it is remarkable that Jeppe returned to the Sahel in May 2012 *before* the onset of the rainy season. At sites F and G, Jeppe experienced the driest (i.e. less green) conditions during the entire period spent in Africa.

We can only speculate why Jeppe left the green area in Guinea-Bissau to return to a very dry area in the Sahel. Conditions in Guinea-Bissau might have been unfavourable for a harrier, or competition with local breeding birds might have increased during the spring. Alternatively, the northward move was initiated as an attempt to migrate, yet never brought Jeppe further than to site F. It is also possible that the Sahel is simply a favourable place for harriers, even when the area is very dry. Indeed, some grasshopper species could be very numerous during dry periods, or the diet of a summering harrier might consist primarily of small mammals, birds and reptiles, and thus be more similar to the typical diet on the breeding grounds.

Sites H and I represent the driest areas visited by Jeppe, and the bird moved to these sites just before or coinciding with the arrival of the summer rains. The bird remained at site I in the northern Sahel throughout the wet season and did not leave until NDVI values dropped markedly. It is very interesting that it opted to spend the rainy season at a site on the northern edge of the Sahel where rains start earlier in the season.

Jeppe's movements during the second winter were quite remarkable. It did not visit the same wintering sites during the two consecutive winters, which contrasts with the site-fidelity typical for Montagu's Harriers in winter (Trierweiler *et al.* 2013), and may indicate that it was exploring unfamiliar territory in order to ultimately increase foraging and survival during subsequent winters. Such explorative behaviour during times of average or high food availability has been described for other bird species (Bennets & Kitchens 2000; Oppel *et al.* 2009); thus the number of sites visited does not necessarily imply that Jeppe was experiencing low food levels.

During the first winter, Jeppe left an area as soon as the NDVI had dropped to the baseline level, and subsequently travelled to a more southern and greener site. This corresponds exactly to the Green Belt hypothesis as described by Trierweiler *et al.* (2013) and Schlaich *et al.* (2016), in which harriers track moderately green vegetation, as this is where the highest densities of grasshoppers are found. In the second winter, however, the last site Jeppe visited had lower NDVI values than the previous sites, suggesting that Jeppe moved to a drier site instead. This is particularly remarkable, since this was the site Jeppe departed from at the onset of spring migration. However, although NDVI values seem to provide a good proxy for grasshopper numbers, sites with similar NDVI values can differ considerably, and site G may have been rich in grasshoppers or alternative prey despite low NDVI. Also noteworthy is the fact that Jeppe had already visited both of the last two sites (A and G) during the first half of his extended stay in Africa, yet during different seasons and presumably under quite different conditions. If Jeppe somehow evaluated these areas and later chose to return, the value of such explorative visits may be quite significant. Therefore, field observations on food abundance are still needed to draw firm conclusions about such aspects.

Conclusions

Our detailed documentation of an adult male Montagu's Harrier over-summering in Africa illustrates that even among adult birds, a trade-off exists between travelling back to Europe for a breeding attempt and staying in Africa to recover. It also shows that remaining in Africa during the summer is generally an option. Daily mortality rates of raptors are highest during spring migration and lowest during winter in Africa (Klaassen *et al.* 2014). Thus, from that perspective, over-summering in Africa might be the best possible option for a migratory bird in suboptimal or poor body condition, or a bird faced with unfavourable weather conditions for migrating. Assuming that mortality rates are lower during summer in Africa than during migration and breeding, over-summering may even result in long-term benefits such as increased familiarity with potential wintering areas. Nevertheless, skipping a breeding attempt is probably a viable option only for long-lived species such as raptors.

Acknowledgements

We dedicate this article to the memory of Michael B. Clausen (1961-2017) and to his son Jeppe. We thank Villum Fonden, The Danish Nature Agency (ref. NST-304-00068) and DOF-BirdLife Denmark's Projekt Hedehøg for financial support to carry out the GPS tracking study in Denmark. In addition, thanks to all Danish farmers collaborating with us to protect the local breeding pairs of Montagu's Harrier, and to Willem Bouten and the UvA-BiTS team for technical advice. Michael B. Clausen, Lars M. Rasmussen and Mathilde Lerche-Jørgensen carried out essential fieldwork. We are grateful to Dr. Steffen Oppel and one anonymous reviewer for constructive comments, and to the Ringing Section at the Natural History Museum of Denmark for providing licenses for trapping and tagging adult Montagu's Harriers.

Compliance with Ethical Standards

The authors declare that they have no conflict of interest.

Capturing, handling and tracking of harriers was carried out under license from the national authority (the Ringing Section at the Natural History Museum of Denmark).

5

A circannual perspective on daily and total flight distances in a long-distance migratory raptor, the Montagu's Harrier *Circus pygargus*

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Abstract

Long-distance migrants are particularly recognized for the distances covered on migration, yet little is known about the distances they cover during the rest of the year. GPS-tracks of 29 Montagu's Harriers from breeding areas in France, The Netherlands and Denmark showed that harriers fly between 35 653 and 88 049 km yr^{-1}, of which on average only 28.5% is on migration. Mean daily distances during migration were 296 km d^{-1} in autumn and 252 km d^{-1} in spring. Surprisingly, males' daily distances during breeding (217 km d^{-1}) were close to those during migration, whereas breeding females moved significantly less (101 km d^{-1}) than males. In terms of flight distance, the breeding season seemed nearly as demanding as migration periods for males. During the six winter months, both sexes moved less (114 and 128 km d^{-1} for females and males, respectively) than during migration. Harriers therefore covered shorter daily distances during winter which might allow birds to compensate for the more demanding phases of migration and breeding.

Background

Migratory lifestyles are considered to have evolved under the premise that benefits of breeding in high-quality seasonal habitats more than outweigh the costs associated with making migratory journeys (Alerstam 1990; Dingle 1980; Newton 2008). However, costs and benefits of migration remain poorly understood, partly because we have little knowledge of the relative costs of migration compared with other phases of the annual cycle (Buehler & Piersma 2008; Klaassen *et al.* 2014; Lok *et al.* 2015). It has been argued that migration is particularly costly since travel distances are relatively large (Klaassen *et al.* 2014; Lok *et al.* 2015), yet most birds also move substantial distances within the breeding and wintering seasons to gather food for themselves and their young. Thus, movements during stationary periods may contribute considerably to the total annual distance covered by birds. How the distance covered during stationary periods scales to migration distance is however largely unknown.

Montagu's Harriers *Circus pygargus* are long-distance migratory raptors with a south-west-Palaearctic breeding and Afrotropical/Indomalayan wintering distribution (Ferguson-Lees & Christie 2001). Migration distance is shorter for more southerly breeding populations, whereas distances travelled in winter and during breeding might depend on habitat quality and food availability (Schlaich *et al.* 2016; Trierweiler *et al.* 2014). Montagu's Harriers forage on the wing, and therefore might cover long distances also during stationary periods (Clarke 1996).

Here we aim at comparing the daily and total flight distances as proxies of energy expenditure during the main phases of the annual life cycle for both sexes of this long-distance migrant, replicated for three breeding populations, using 40 complete annual cycles of 29 Montagu's Harriers followed by GPS trackers.

Material and methods

GPS-tracking data

We collected data for 40 complete annual cycles (from 1 July until 30 June the following year) of 9 female and 20 male Montagu's Harriers tracked by means of UvA-BiTS GPS trackers (www.uva-bits.nl; Bouten *et al.* 2013) between 2009 and 2016. Seven individuals were tracked during 2 and two individuals during 3 years. Birds originated from breeding areas in Denmark (n = 3), The Netherlands (18) and France (8). GPS trackers were mounted using a Teflon ribbon harness and programmed to collect GPS positions at intervals of 5 min (n = 7 tracks), 10 min (12), 15 min (16), or 30 min (5) during daytime and a maximum of once per hour at night during migration and winter. During breeding, higher frequencies were obtained (most common interval was 5 min, but additional bursts of high-resolution data (3 s) were collected) but tracks were subsampled to the most common interval for the whole year. Data were checked for outliers visually on a map and points for which instantaneous or trajectory speed was higher than 30 m s^{-1} were deleted (453 fixes deleted, 1 134 664 fixes remained for analyses). Using a map of the recorded positions, daily tracks were assigned

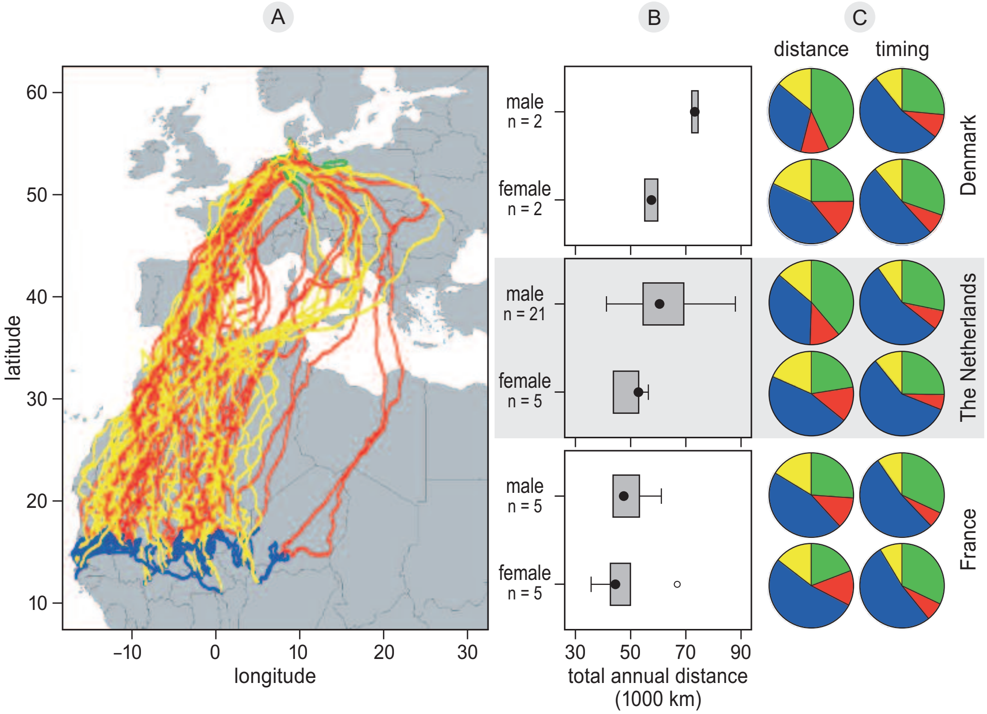

Figure 5.1. (**A**) Map showing all tracks with colours indicating annual cycle phases (green = breeding, red = autumn migration, blue = winter, yellow = spring migration). (**B**) Total annual distance flown by female and male Montagu's Harriers from France, The Netherlands and Denmark during 1 year. Number of tracks per sex is given besides boxplots. (**C**) Pie charts depicting fraction of distance and time per annual cycle phase separated for populations and sexes. For individuals with repeated journeys the average value was used. Colours as in (**A**).

annual cycle phases (breeding, autumn migration, wintering, spring migration; Fig. 5.1). Pre- and post-migratory movements (Strandberg *et al.* 2008) were assigned to the nearest stationary period (pre-autumn (n = 8) and post-spring (n = 4) to breeding, post-autumn (n = 16) to winter). Daily distance was calculated by adding the distances between consecutive positions using function *distMeeus* from R package *geosphere* version 1.5-5 (Hijmans 2015). Cumulative distance for each annual cycle phase was the sum of all daily distances within the phase and total annual distance was the sum of all daily distances within the whole year.

Interval bias correction

Adding straight-line distances between GPS positions underestimates true distance travelled depending on sampling interval and tortuosity of the movement path (Pépin *et al.* 2004; Rowcliffe *et al.* 2012). To correct for this effect, we subsampled high-resolution tracks (1200 fixes per hour) to intervals of 600, 300, 150, 75, 37.5, 18.75, 12, 6, 4, 3 and 2 fixes per hour (for an example see electronic supplementary material, Fig. S1). High resolution data were regularly collected during breeding, but rarely during migration and winter owing to limited memory storage. In total, we accumulated 16.5 h for autumn migration, 11.5 h for spring migration, 11 h for winter and 14 h for breeding from tracks of Dutch male Montagu's Harriers. By recalculating straight-line distances between GPS positions for each subsampled dataset we calculated proportional accuracy (ratio of apparent to true distance travelled) using the original 1200 fixes per hour distance as reference (electronic supplementary material, Fig. S2). Daily distance was then corrected according to sampling interval of the track and annual cycle phase by multiplying with a correction factor (mean (range) breeding: 4.08 (2.73–7.79), autumn migration: 1.32 (1.24–1.36), winter: 3.30 (2.56–3.99), spring migration: 1.35 (1.27–1.43)). Correction factors are higher during stationary periods owing to more tortuous movements compared with directed flights during migration (cf. electronic supplementary material, Fig. S1). This correction might overestimate distances for females during breeding (incubation) and for birds moving between sites in winter or on stopover days.

Statistical analyses

In order to test for differences between the sexes and populations regarding total annual distance, daily distance, and cumulative distance, we used linear mixed models (LMMs) with function *lme* from package *nlme* version 3.1-127 (Pinheiro *et al.* 2016) in R version 3.3.0 (R Core Team 2016). In all models we included *individual* as random effect and *population* and *sex* as fixed effects. In the annual cycle phase-specific estimates we also included *phase* and the interaction terms *phase:sex* and *phase:population* as fixed effects. This resulted from comparing models with all possible combinations of interaction terms using the Akaike information criterion (AIC). Multi-comparison post-hoc tests were performed to evaluate differences between populations and annual cycle periods using R-function *testInteractions* from package *phia* version 0.2-1 (De Rosario-Martinez 2015). Estimates were calculated using R-function *allEffects* from package *effects* version 3.1-2 (Fox 2003).

Results and discussion

Montagu's Harriers travelled on average 57 841 km (range 35 653–88 049 km) per year. Males travelled about 20% more than females (Table 5.1*a*, Fig. 5.1; mean values: males 61 071 km, females 50 305 km), mainly because males covered longer daily distances during the breeding season compared with females (217 and 101 km day^{-1}, respectively; Table 5.1*b*, Fig. 5.2; cf. electronic supplementary material, Fig. S3 for individual time-series). This difference results from males provisioning the incubating female and both chicks and female during the first weeks after hatching (Clarke 1996). Interestingly, despite female Montagu's Harriers being substantially larger (370 versus 260 g), and therefore needing more food, we found no significant difference in winter flight distance (Table 5.1*b*, Fig. 5.2; mean values: males 114 km day^{-1}, females 128 km day^{-1}). This might either indicate that food availability in general is not limiting or hint towards differential prey choice of the sexes during winter.

French birds travelled less than Dutch and Danish birds (Table 5.1*a*, Fig. 5.1; post-hoc test in electronic supplementary material, Table S2*a*), mainly because French males flew less during breeding (Table 5.1*b*, Fig. 5.2; mean values: F 92, NL 211, DK 217 km day^{-1}) and not due to their shorter migration routes. It remains to be investigated whether this is caused by varying habitat quality and food availability.

Whereas 17% of the year was allocated to migration, birds covered 28.5% of their annual distance during this period (Figs. 5.1 and 5.2; females 31%, males 26%). Migration is often seen as an exceptional investment, but interestingly, males reached nearly similar daily distances during breeding as during migration. When comparing these daily distances to seasonal variation in mortality rates derived from satellite telemetry (Klaassen *et al.* 2014), it is striking that daily mortality rates during breeding (0.0012) are considerably lower than during autumn (0.0023) or spring migration (0.0052). Therefore, high mortality rates during migration are unlikely to be related to endurance of long-distance flight *per se*. Instead, it was suggested that high mortality rates during migration were related to unfavourable conditions encountered during migration and, possibly, to carry-over effects of demanding breeding seasons (Klaassen *et al.* 2014). During the six winter months, Montagu's Harriers fly relatively short daily distances and mortality is at its lowest (0.0006; Klaassen *et al.* 2014). Studies on other migratory species confirm that the wintering period seems to be the least demanding as survival rates are comparatively high (Blackburn & Cresswell 2016a; Sillett & Holmes 2002). Still, deteriorating environmental conditions in the course of the

Table 5.1. Results of analyses of variance of LMMs on (**A**) total annual distance, (**B**) mean daily distance and (**C**) cumulative distance of male and female Montagu's Harriers from France (n = 10), The Netherlands (n = 26) and Denmark (n = 4 tracks). All models included i*ndividual* as random effect and *population* (F, NL and DK) and sex (female, male) as fixed effects. In (**B**) and (**C**) we also tested *phase* (breeding, autumn migration, winter, spring migration) and all (two- and three-way) interaction terms. Models were compared using the Akaike information criterion (AIC) and output of the model with the lowest AIC is shown. All estimates can be found in the electronic supplementary material, table S1.

Variable	**edf**	***F*-value**	***P*-value**
(*a*) total annual distance (km) (LMM, figure 5.1, estimates electronic supplementary material table S1)			
intercept	25	966.94	<0.001
sex	25	6.46	0.02
population	25	3.84	0.04
(*b*) mean daily distance (km) (LMM, figure 5.2A, estimates electronic supplementary material table S1)			
intercept	119	1337.3	<0.001
phase	119	71.85	<0.001
sex	25	2.71	0.11
population	25	2.4	0.11
phase × sex	119	10.55	<0.001
phase × population	119	2.56	0.02
(*c*) cumulative distance (km) (LMM, figure 5.2C, estimates electronic supplementary material table S1)			
intercept	119	894.16	<0.001
phase	119	112.79	<0.001
sex	25	6.13	0.02
population	25	3.39	0.05
phase × sex	119	18.08	<0.001
phase × population	119	2.67	0.02

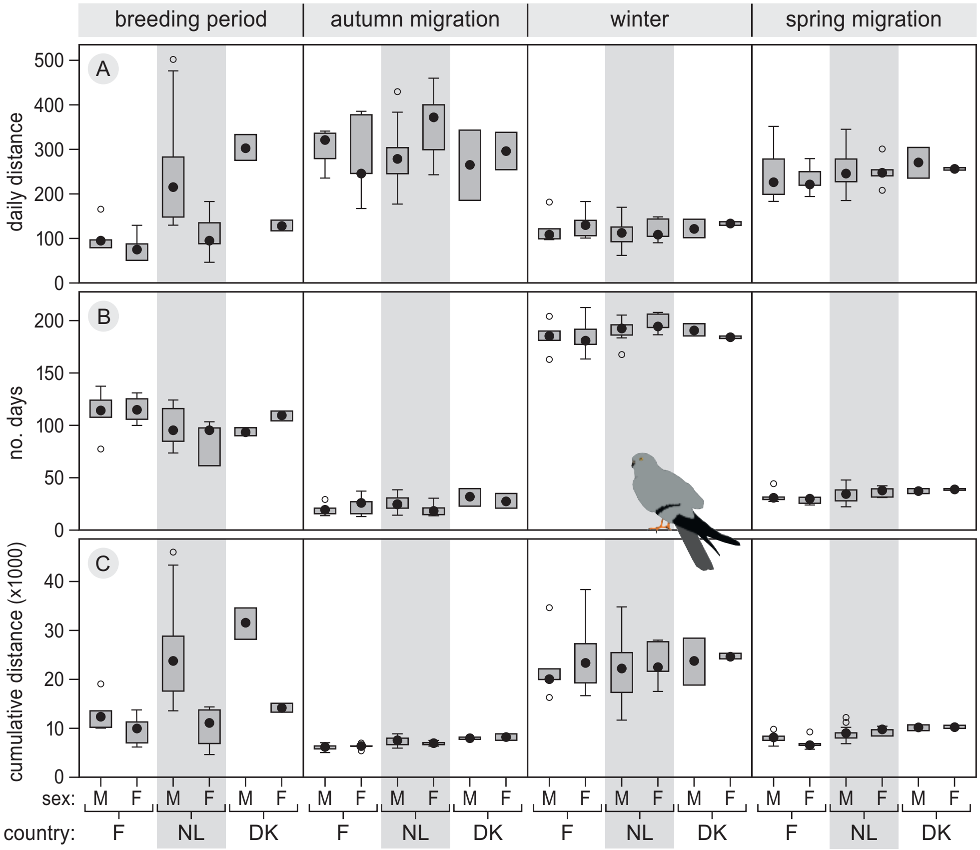

Figure 5.2. (**A**) Mean daily distance (km), (**B**) number of days and (**C**) cumulative distance (km) during the four main annual cycle periods for male and female Montagu's Harriers originating from breeding populations in France, The Netherlands and Denmark. Boxplots show between-individual variance using the mean value per individual. For sample sizes see figure 5.1.

Sahelian winter force harriers to increase foraging time, and thereby daily distance travelled, and cause delays in spring departure for individuals wintering at the driest sites (Schlaich *et al.* 2016).

How general is the pattern of long-distance migrants flying daily distances during migration nearly similar to those during other annual cycle periods? We consider it likely that species hunting on the wing, like swallows, swifts, seabirds and many raptors, may cover similar distances during stationary and migratory periods, whereas for birds foraging on the ground or in the foliage, migration may indeed be outstanding in terms of daily flight distances. It is important to mention that recording interval strongly affects estimated distance and thus high frequency tracks are required (Rowcliffe *et al.* 2012; Dewhirst *et al.* 2016). Earlier reports on daily travel distances of Montagu's Harriers using satellite tracking data (autumn 175 km day^{-1}, spring 166 km day^{-1}; Trierweiler *et al.* 2014) or lower resolution GPS-tracking data (autumn 205 km day^{-1}, spring 182 km day^{-1}; Vansteelant *et al.* 2015) were indeed 28-35 % lower than our corrected calculations using high-resolution tracks (autumn 296 km day^{-1}, spring 252 km day^{-1}).

To place migration into a life-history perspective, we consider it essential to compare the investment with that in other life cycle phases, as performed here for harriers using distance as a proxy for energy expenditure. Our main findings show that daily distances of breeding males are almost comparable to daily distances flown during migration, but that winter is less demanding. However, we need to investigate at what cost this comes, and whether effects carry over to survival, reproductive success and even population dynamics. This might become more important with further intensification of agricultural landscapes making breeding even more demanding owing to decreasing habitat quality and food availability.

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Ethics

Tracking was approved by local ethical committees: University of Groningen, Tthe Netherlands (permits 5869B and 6429B), the Natural History Museum of Denmark, and CRBPO Muséum National d'Histoire Naturelle for France (permit 1308).

Data accessibility

Data are available from the Dryad Digital Repository: doi:10.5061/dryad.84jk0 [24].

Authors' contributions

Fieldwork: A.E.S., R.H.G.K., I.H.S., A.V. Data-analysis and processing: A.E.S., W.B., C.B. Local project coordination: V.B., H.H. Drafting manuscript: A.E.S., C.B. All authors helped edit and revise the manuscript, gave final approval for publication and agreed to be held accountable for the content therein.

Competing interests

We have no competing interests.

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Supplemental material

Table S1. Estimates of all factor levels from models given in Table 5.1.

Variable	Estimate	se	Lower	Upper
(A) total annual distance (km)				
sex				
female	50978.3	3454.8	43971.6	57985.0
male	60807.5	2250.6	56243.0	65372.0
population				
France	49987.9	3616.8	42652.6	57323.2
Netherlands	59523.8	2364.7	54728.0	64319.5
Denmark	66713.0	5905.9	54735.3	78690.7
(B) mean daily distance (km)				
phase:sex				
breeding-female	113.5	18.6	76.7	150.3
autumn migration-female	320.7	18.6	283.9	357.5
winter-female	125.0	18.6	88.2	161.8
spring migration-female	246.1	18.6	209.3	282.9
breeding-male	212.4	12.0	188.7	236.1
autumn migration-male	285.8	12.0	262.2	309.5
winter-male	116.5	12.0	92.8	140.2
spring migration-male	255.8	12.0	232.1	279.5
phase:population				
breeding-France	111.1	20.0	71.6	150.7
autumn migration-France	285.6	20.0	246.0	325.1
winter-France	125.1	20.0	85.6	164.7
spring migration-France	242.1	20.0	202.6	281.7
breeding-Netherlands	202.1	12.5	177.4	226.8
autumn migration-Netherlands	304.1	12.5	279.3	328.8
winter-Netherlands	115.7	12.5	91.0	140.4
spring migration-Netherlands	255.3	12.5	230.6	280.0
breeding-Denmark	235.8	31.5	173.6	298.0
autumn migration-Denmark	272.8	31.5	210.6	335.0
winter-Denmark	126.0	31.5	63.8	188.2
spring migration-Denmark	264.1	31.5	201.9	326.3
(C) cumulative distance (km)				
phase:sex				
breeding-female	11511.2	1499.2	8547.8	14474.6
autumn migration-female	6954.4	1499.2	3991.0	9917.8
winter-female	23987.7	1499.2	21024.3	26951.1
spring migration-female	8580.2	1499.2	5616.8	11543.5
breeding-male	22883.6	965.5	20975.1	24792.0
autumn migration-male	7177.4	965.5	5269.0	9085.9
winter-male	22054.8	965.5	20146.3	23963.2
spring migration-male	8641.5	965.5	6733.0	10549.9

Table S1. Continued.

Variable	Estimate	se	Lower	Upper
(C) cumulative distance (km)				
phase:population				
breeding-France	13443.8	1608.3	10264.8	16622.7
autumn migration-France	6086.7	1608.3	2907.8	9265.7
winter-France	23305.4	1608.3	20126.5	26484.4
spring migration-France	7364.4	1608.3	4185.4	10543.3
breeding-Netherlands	20936.6	1007.6	18945.0	22928.2
autumn migration-Netherlands	7366.8	1007.6	5375.2	9358.4
winter-Netherlands	22209.6	1007.6	20218.0	24201.2
spring migration-Netherlands	8877.9	1007.6	6886.3	10869.5
breeding-Denmark	25021.1	2535.1	20010.3	30031.9
autumn migration-Denmark	8004.0	2535.1	2993.2	13014.8
winter-Denmark	23720.8	2535.1	18710.0	28731.6
spring migration-Denmark	10113.4	2535.1	5102.6	15124.2

Table S2. Model output of post-hoc tests on total annual distance between populations, as well as mean daily distance and cumulative distance between annual cycle phases.

Variable	Estimate	χ^2-value	*P*-value
(A) post-hoc test population differences total annual distance (km)			
F-NL	−9535.8	4.77	0.06
F-DK	−16725.1	5.99	0.04
NL-DK	−7189.3	1.25	0.26
(B) post-hoc test phase differences mean daily distance (km)			
breeding-autumn migration	−131.18	5.96	<0.001
breeding-winter	39.27	5.11	0.03
breeding-spring migration	−88.64	26.01	<0.001
autumn migration-winter	170.46	96.18	<0.001
autumn migration-spring migration	42.54	5.99	0.03
winter-spring migration	−127.92	54.16	<0.001
(C) post-hoc test phase differences cumulative distance (km)			
breeding-autumn migration	10418.1	57.23	<0.001
breeding-winter	−5939.2	18.60	<0.001
breeding-spring migration	8753.1	40.40	<0.001
autumn migration-winter	−16357.3	141.08	<0.001
autumn migration-spring migration	−1665.1	1.46	0.23
winter-spring migration	14692.2	113.82	<0.001

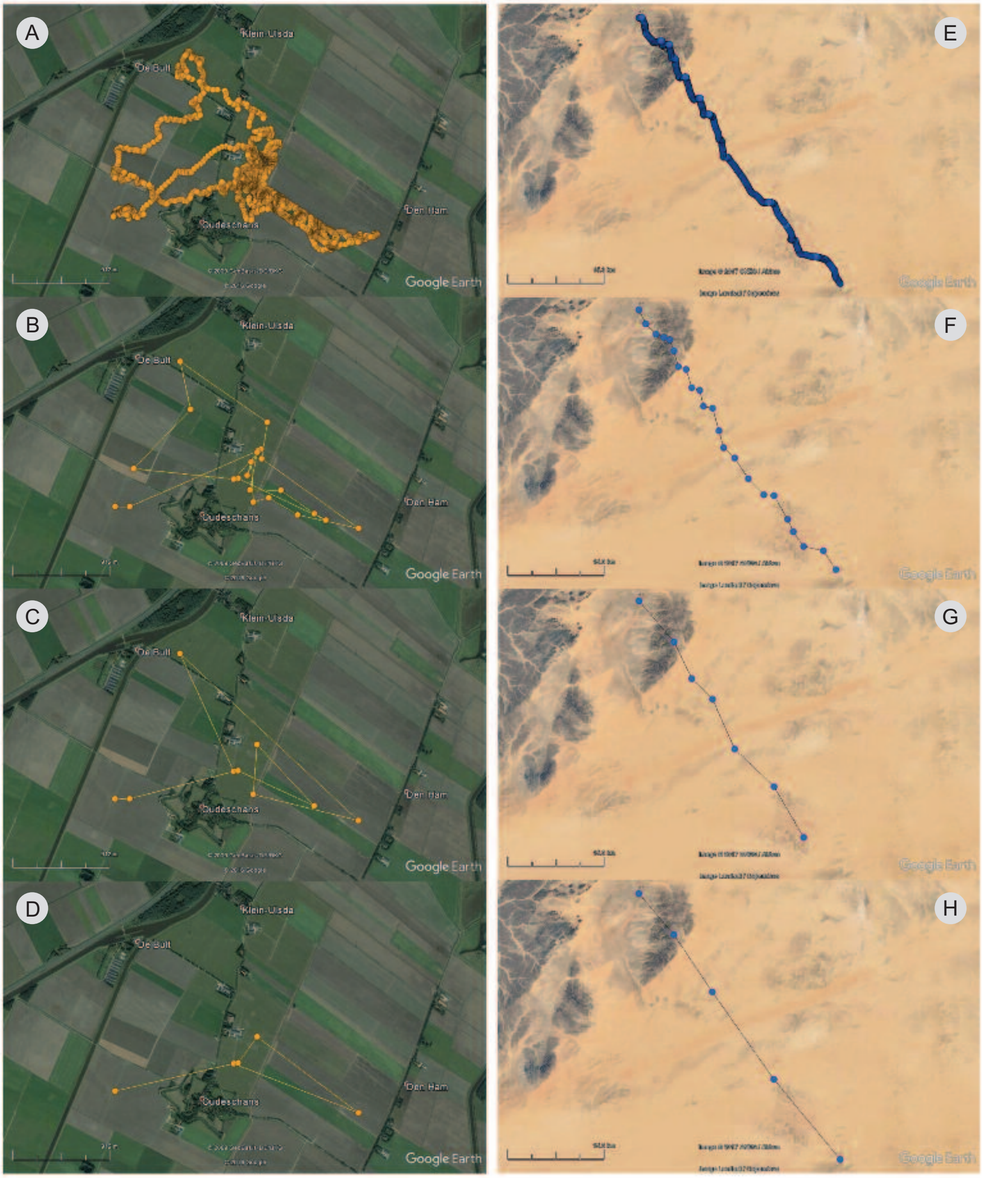

Figure S1. (**A**) Two hours of high-resolution (3 seconds interval) track of male Montagu's harrier Elzo (ID 428) on 24 May 2012 during the breeding season in the Netherlands. Same track subsampled to (**B**) 5 min, (**C**) 15 min, and (**D**) 30 min interval. Distances calculated between consecutive positions: (**A**) 30.4 km, (**B**) 10.4 km, (**C**) 7.7 km, (**D**) 3.9 km. (**E**) Two hours of high-resolution (3 seconds interval) track of male Montagu's harrier Elzo (ID 428) on 19 September 2011 during autumn migration crossing the Sahara desert. Same track subsampled to (**F**) 5 min, (**G**) 15 min, and (**H**) 30 min interval. Distances calculated between consecutive positions: (**E**) 65 km, (**F**) 56 km, (**G**) 46 km, (**H**) 53 km.

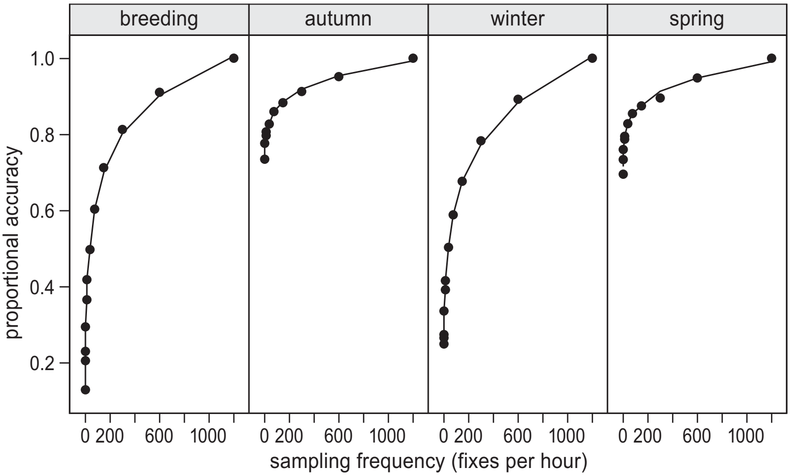

Figure S2. Proportional accuracy (ratio of apparent to true distance travelled) in relation to sampling frequency for GPS-tracked Montagu's Harriers. The nonlinear least-squares estimates of the parameters were estimated fitting a non-linear model ($y = ax^b + c$) using R-function *nls* (breeding: $y = 330.57x^{0.036} - 324.41$; autumn migration: $y = 27.38x^{0.1} + 43.9$; winter: $y = 47.16x^{0.142} - 28.41$; spring migration: $y = 22.68x^{0.117} + 47.35$).

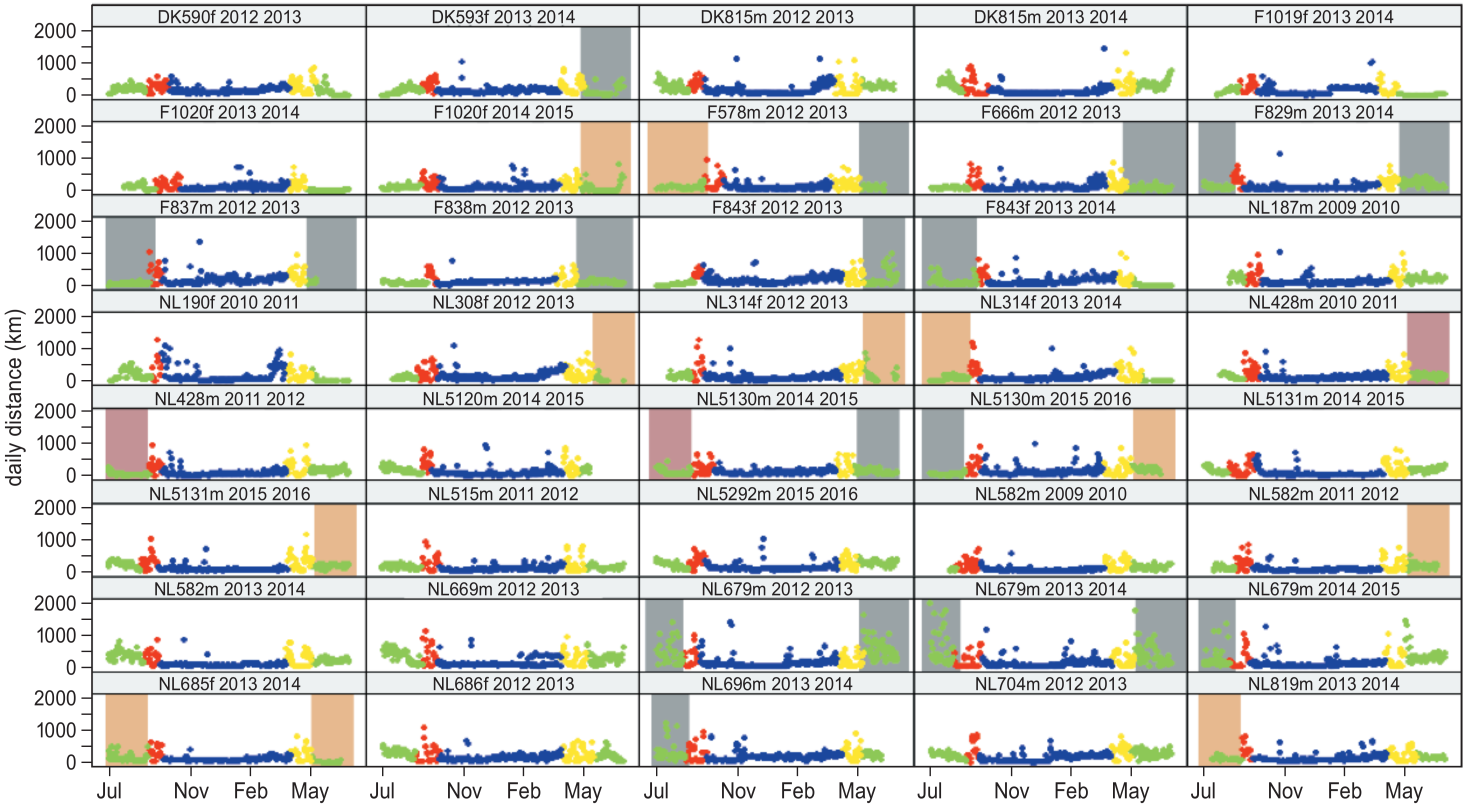

Figure S3. Daily distance travelled by Montagu's Harriers tracked by GPS trackers during a whole annual cycle. Names of individuals are composed of country acronym (DK = Denmark, F = France, NL = Netherlands), the GPS-tracker ID, sex of the bird (f = female, m = male), and the years considered (data from 1 July in year 1 to 30 June in year 2). Colours indicate annual cycle phases (green = breeding, red = autumn migration, blue = winter, yellow = spring migration). Background colours indicate breeding fate (gray = non-breeder, orange = nest failure during egg phase, red = nest failure during chick phase). Distances were corrected according to sampling interval and annual cycle phase.

6

Individual variation in home range size reflects different space use strategies in a central place foraging raptor bird

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Abstract

The home range is a fundamental concept in ecology, but individual variation in home range size remains poorly understood. We tracked 14 male Montagu's Harriers during the breeding season using GPS trackers, providing an unprecedented detailed account on daily, seasonal and annual variation in movements, space use and home range size in relation to environmental conditions such as weather, food availability, and habitat. Despite breeding in the same areas, individuals varied five-fold in home range size, reflecting different space use strategies. Individuals with relatively small home ranges moved relatively little and exploited a few high-quality foraging patches which they re-visited frequently. Individuals with relatively large home ranges moved longer distances, rarely re-visited patches but explored new patches instead. The unique approach of studying variation in movement and space use at different spatiotemporal scales, from within-individual daily variation to between-individual seasonal variation, provides a novel perspective on home range size variation.

Introduction

The home range is defined as 'that area traversed by the animal during its normal activities of food gathering, mating, and caring for young' (Burt 1943). It is a basic concept in ecology as it forms the direct link between the behaviour of the animal and the landscape, including the distribution of resources (Börger *et al.* 2006b). Space use within home ranges is not uniform as animals typically use certain sites more intensively than others (Jennrich & Turner 1969; Ford & Krumme 1979; Benhamou & Riotte-Lambert 2012). Patterns in space use (e.g. habitat selection) are informative about the ecological requirements of the species, and this knowledge is ultimately required to design effective conservation measures (Sutherland 1998).

Home range size is influenced by a myriad of factors, such as habitat composition, food abundance, weather, and season (Börger *et al.* 2006b; Kenward 1982; Village 1982; Marquiss & Newton 1981; Rutz 2006; Saïd *et al.* 2009; Van Beest *et al.* 2011). In addition, notable differences in space use exist between individuals (Börger *et al.* 2006b; Saïd *et al.* 2009; Van Beest *et al.* 2011; Campioni *et al.* 2013), which might reflect differences in animal personalities (Van Overveld & Matthysen 2010). However, relatively little is known about individual variation in home range size and, in particular, about factors causing this variation (Saïd *et al.* 2009). Indeed, various authors have emphasized that intraspecific variation in home range size is less well understood than interspecific variation (Börger *et al.* 2006b; Kjellander *et al.* 2004).

One of the reasons why intraspecific variation in home range size remains understudied might be that it hitherto was difficult to map space use of individual animals in sufficient detail. For example, space use has traditionally been studied by tracking animals using radio-transmitters (Kenward 1987), but as this technology provides just a limited number of positions per day it was only suitable to study total (overall) home range size (providing the basis for interspecific comparisons). Recent technological developments of smaller and more sophisticated tracking devices allows studying movement and space use of wild animals in their natural environment at unmatched small spatial and temporal resolution, revolutionizing our understanding of fundamental aspects of animal ecology, including home range size and habitat use (Rutz & Hays 2009; Ropert-Coudert & Wilson 2005; Kays *et al.* 2015).

We studied individual variation in space use and home range size in a diurnal raptor, the Montagu's Harrier *Circus pygargus*, by tracking 14 individual male harriers using state-of-the-art GPS-tracking technology (Bouten *et al.* 2013). The motivation for this study was to improve conservation efforts for this vulnerable farmland bird species (EBD 2009; Koks *et al.* 2007; Schlaich *et al.* 2015). GPS trackers were programmed to collect GPS positions every five minutes during the day, providing about 180 positions per day.

Thanks to the vast amount of accurate tracking data collected, per individual and per day, we were in the unique position to study variation in movement, space use and home range size at different temporal scales, from within-individual daily variation to between-individual seasonal variation (Harris *et al.* 1990). In order to understand factors explaining variation in movement and space use, we related daily variation in movement, space use and home range size to weather and to the harriers' breeding phase (i.e. different phases of the harrier's breeding cycle). In addition, we related individual variation in total home range size to annual fluctuations in food availability (abundance of Common Voles *Microtus arvalis*, the harriers' main food in the study area (Koks *et al.* 2007)) and habitat use. Moreover, the vast amount of tracking data allowed us to additionally analyse space-use patterns within home ranges, and we developed a new approach to quantify the intensity of the use of different sites within the home range. By relating within home range space-use patterns to the total home range size and habitat use, we provide a novel perspective on home range size variation.

Material and methods

Study system

The Montagu's Harrier is a migratory raptor breeding in farmland (Arroyo 2004). We study a small breeding population of about 30–50 pairs (Koks *et al.* 2007) in northeast Groningen, The Netherlands (latitude: 53.12° N, longitude: 7.08° E). This area is dominated by intensive agriculture (Koks *et al.* 2007). On the clayey soils in the east and north of the study area, land use is dominated by winter cereals (mainly winter wheat), interspersed with rapeseed, grassland and beetroots. On sandier soils in the south and southeast the main crops are potatoes, beetroots, summer cereals, maize, and grassland. The harrier population established in this area in 1990-1993 when large areas were left fallow, and subsequently increased after the large-scale implementation of Agri-Environment Schemes (AES) (since 1997), partly specifically targeted at Montagu's Harriers (Koks *et al.* 2007; Schlaich *et al.* 2015).

In this study, we focus on movement and space use of male Montagu's Harriers. During the breeding season, males are central place foragers (Orians & Pearson 1979), regularly returning to the nest to deliver prey (Clarke 1996). Females only start to contribute to food provisioning during the second half of the nestling stage (Clarke 1996). Males are not territorial although they defend the direct vicinity of their nest (Clarke 1996).

Tracking details

Montagu's Harriers were captured near the nest either using a mist net in combination with a stuffed raptor, or by using a snare-trap mounted on a perch. Birds were fitted with 12–14 gram UvA-BiTS GPS trackers (Bouten *et al.* 2013) using a full-body harness made from 6 mm wide Teflon strings (Kenward 1987), and were released within 20–40 minutes after capture. We never observed nest desertion or failure in relation to capture events.

In total, 22 adult male Montagu's Harriers were tagged in 2011–2014. However, birds did not always attempt to breed, or breeding attempts failed prematurely. The remaining dataset comprised of 20 annual home ranges from 14 individuals (Fig. 6.1A & Table S1). Five individuals were tracked during multiple breeding seasons: four birds during two seasons and one bird during three seasons.

GPS trackers were programmed to collect GPS positions every five minutes between 5:00 and 20:00 GMT, which covers the main period of activity of Montagu's Harriers during the breeding season. This was the highest possible sampling frequency which did not deplete internal batteries even on rainy days. During periods with favourable weather conditions,

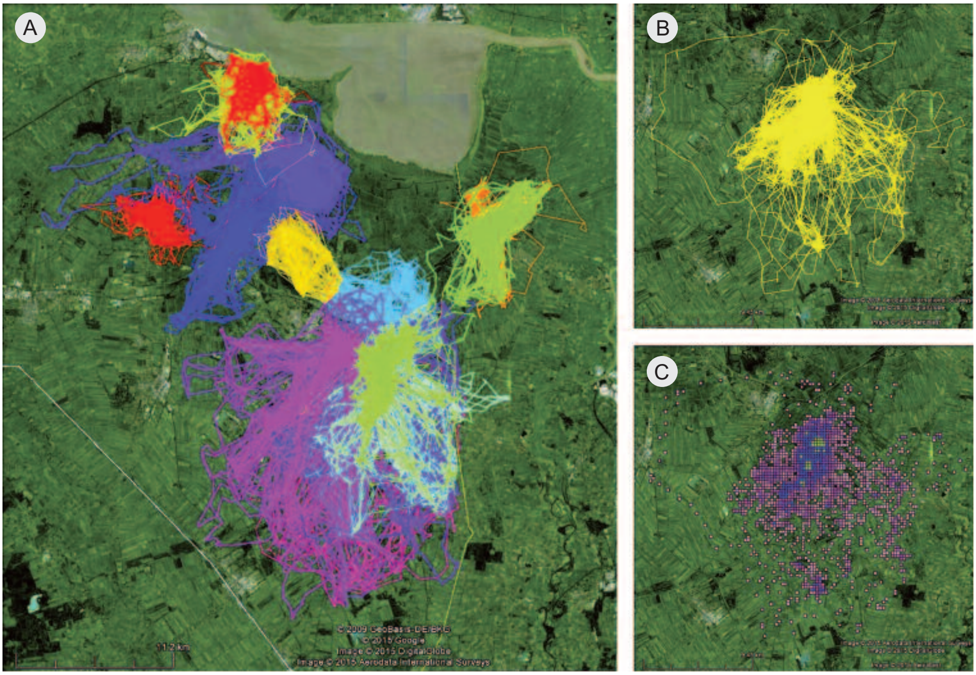

Figure 6.1. (**A**) 20 different tracks of 14 adult male Montagu's Harriers during the breeding season. Only data for the nestling phase is shown. Colours correspond to Fig. 6.4A. (**B**) Example of a track and (**C**) corresponding cumulative use of 250 × 250m squares. Colouration reflects the intensity of use of a square.

hourly bouts of high-frequency data (GPS fixes every 3 sec) were collected, but these data were sub-sampled to 5 minute intervals for the current analysis. The remaining dataset contained 215,505 GPS positions.

Data analysis

A 'season' is the whole period the bird was present in the study area in a particular year (individuals thus could be tracked during different seasons). Seasons were subdivided in four breeding phases: pre-breeding, incubation (female incubating eggs), nestling (young in nest), and post-fledging (young fledged) period. Timing of the breeding phases was back-calculated from the age of the young upon ringing, as calculated from the relationship between wing length and age (Bijlsma 1997), and assuming an incubation period of 29 days (Bijlsma 1997). In some cases the breeding attempt failed, for example because the nest was depredated, and thus not all 'seasons' are complete (see Table S1).

For the current analysis we were only interested in the behaviour during the day, thus only daytime positions were selected. In addition, only days were included for which more than 100 GPS fixes were obtained in order to avoid problems with varying sample sizes between days (Harris *et al.* 1990; Börger *et al.* 2006a). We nevertheless included the number of fixes per day in our statistical models to correct for possible effects of sample size (see below).

For every GPS fix, we determined whether the bird was flying or sitting based on the instantaneous speed, using a threshold of 2 m s^{-1} (Fig. S1). For less than 1% of all GPS fixes no information on the instantaneous speed was available and hence no speed class could be determined (categorized as “unknown”). Subsequently, we calculated, for every day, the proportion of time the individual bird was flying. The cumulative distance covered per day was calculated by summing the distances between subsequent GPS fixes.

In order to calculate home range size we divided the study area in 250 × 250 m squares, and calculated the number of squares visited per day (daily home range size) and during the nestling phase (referred to as ‘total home range size’) (Fig. 6.1B,C). A square size of 250 × 250 m was chosen as this reflects the spatial resolution of the study area (i.e. matches average field size). Smaller and larger square sizes (100 × 100 m to 500 × 500 m) gave qualitatively similar results. Overlap between daily home ranges was calculated as the number of squares visited on both days divided by the total number of squares visited on those days. This overlap was calculated for different time lags between days, ranging from 1 to 10 days. Finally we calculated the number of days the different squares were visited, which was summarized in a frequency distribution of visiting frequencies. Note that we consider the whole area used during the day, including the nest, as the home range of the animal.

Weather data, hours of rain per day and daily cumulative solar radiation, were obtained from a nearby weather station in Nieuw Beerta (latitude: 53.196°, longitude: 7.150°; Koninklijk Nederlands Meteorologisch Instituut, KNMI, www.knmi.nl/kennis-en-datacentrum/). Duration of rain was believed to be a better predictor of activity than the absolute amount of rain. We assume that daily solar radiation forms a proxy for favourable soaring conditions.

Voles were monitored in late summer (July-August) by counting the number of burrows within 2 × 100 m transects (Schlaich *et al.* 2015). Vole numbers were counted in different habitats, but for this analysis only grassland was considered, as grassland is the single most important foraging habitat in our study area (see ‘Results’, Wiersma *et al.* 2014) and the most frequently monitored habitat. 87 fields were monitored in 2011, 127 in 2012, 75 in 2013, and 54 in 2014. Six transects were counted per field, two in the middle and four along the edges. Here, only the two mid-field transects were considered to exclude edge-effects. Data were averaged per field.

Habitat data was obtained from Wiersma *et al.* (2014). They compiled detailed land use maps for the study area, at the resolution of individual fields. The basis of their inventory were annual field use maps from the Netherlands Enterprise Agency (“Dienst Regelingen”, www.rvo.nl), complemented with specific data on AES from the Province of Groningen (“Collectief Beheerplan”), local farmer associations, and own observations. No such detailed compilation was available for 2013-2014, thus habitat analyses are restricted to 2011-2012. Field use was grouped into seven main categories: (1) winter and summer cereals: wheat, barley, rye, etc., (2) root crops, rapeseed and maize: beets, potatoes, maize, rapeseed, (3) grassland and alfalfa, (4) set-aside AES: field strips, winter food plots, birdfields, (5) unintended set-aside: wasteland with habitat characteristics very similar to AES, (6) natural areas: nature reserves, and (7) other and unknown: roads, buildings, rare habitats, etc. In the study area two large patches of unintended set-aside were found; the dredging depots of the harbour of Delfzijl and the undeveloped area of the 'Blauwe Stad' housing development project near Winschoten.

Statistical analyses

A linear mixed effect model (LMM) approach was adopted in which statistical significance was obtained by likelihood ratio tests of the full model including the dependent variable in question against the reduced model excluding the variable (Zuur *et al.* 2009). Inspection of residual plots did not reveal homoscedasticity or deviations from normality. All analyses were performed in R (R Core Team 2014), using the *lme4* package (Bates *et al.* 2014). Details on sample sizes for seasons and breeding phases are provided in Table S1.

The effect of breeding phase was analysed with *time flying per day*, *distance per day*, or *daily home range size* as dependent variables. Fixed and continuous factors included were *breeding phase*, *weather* (*hours of rain per day* or *daily cumulative solar radiation*, see below), and *number of GPS positions per day*. Random factors included were *season*, *individual* and *year*. In this analysis, only data for seasons were included for which at least 10 days of data for at least three different breeding phases were obtained (Table S1; final dataset comprised of 10 seasons from 7 individuals).

To analyse the effect of weather we focussed on the nestling phase only as this warranted a more detailed analysis including a larger sample of seasons and individuals. Only seasons with at least 14 days of data were included (Table S1; final dataset comprised of 20 seasons from 14 individuals). Dependent variables were *time flying per day*, *distance per day*, or *daily home range size*. Fixed and continuous factors included were *weather* (*hours of rain per day* or *daily cumulative solar radiation*, see below), and *number of GPS positions per day*. Random factors included were *season*, *individual* and *year*.

The effect of individual and year on the total home range size during the nestling phase were analysed with *total home range size* as dependent variable. The model testing for an effect of *individual* included *year* as random factor and the model testing for an effect of *year* included *individual* as random factor. In this analysis, only data for seasons with at least 14 days of data for the nestling period were included.

The relationship between the proportion of set-aside in the habitat and total home range size was analysed with *total home range size* as dependent variable and *proportion of set-aside* as continuous variable. Random factors included were *individual* and *year*. In this analysis, only data for 2011–2012 were included as no habitat maps were available for 2013–2014.

Results are only presented for models including *duration of rain* as weather variable, except if explicitly stated, as *duration of rain* and *daily solar radiation* were correlated (correlation coefficient: –0.57). In all cases, results were similar if *rain duration* was replaced by *daily solar radiation*.

Individual repeatability of daily home range size between years was analysed using the *rptR* package (Stoffel *et al.* 2017) following recommendations by (Nakagawa & Schielzeth 2010). This analysis was based on the same dataset as for the analysis of effects of weather (see above).

Results

Variation in movement, space use and home range size

Proportion of time flying per day, cumulative distance travelled per day, and daily home range size were strongly correlated (Fig. S2). Individuals differed significantly in the time flying per day, cumulative distance travelled per day, and daily home range size ($\chi^2_{13} = 43.5$, $P < 0.001$; $\chi^2_{13} = 41.5$, $P < 0.001$; $\chi^2_{13} = 42.2$, $P < 0.001$), as well as in total home range size ($\chi^2_{13} = 52.3$, $P < 0.001$, Fig. 6.4A).

Proportion of time flying per day, cumulative distance travelled per day, and daily home range size varied between breeding phases (Fig. 6.2, $\chi^2_3 = 314.5$, $P < 0.001$; $\chi^2_3 = 250.2$,

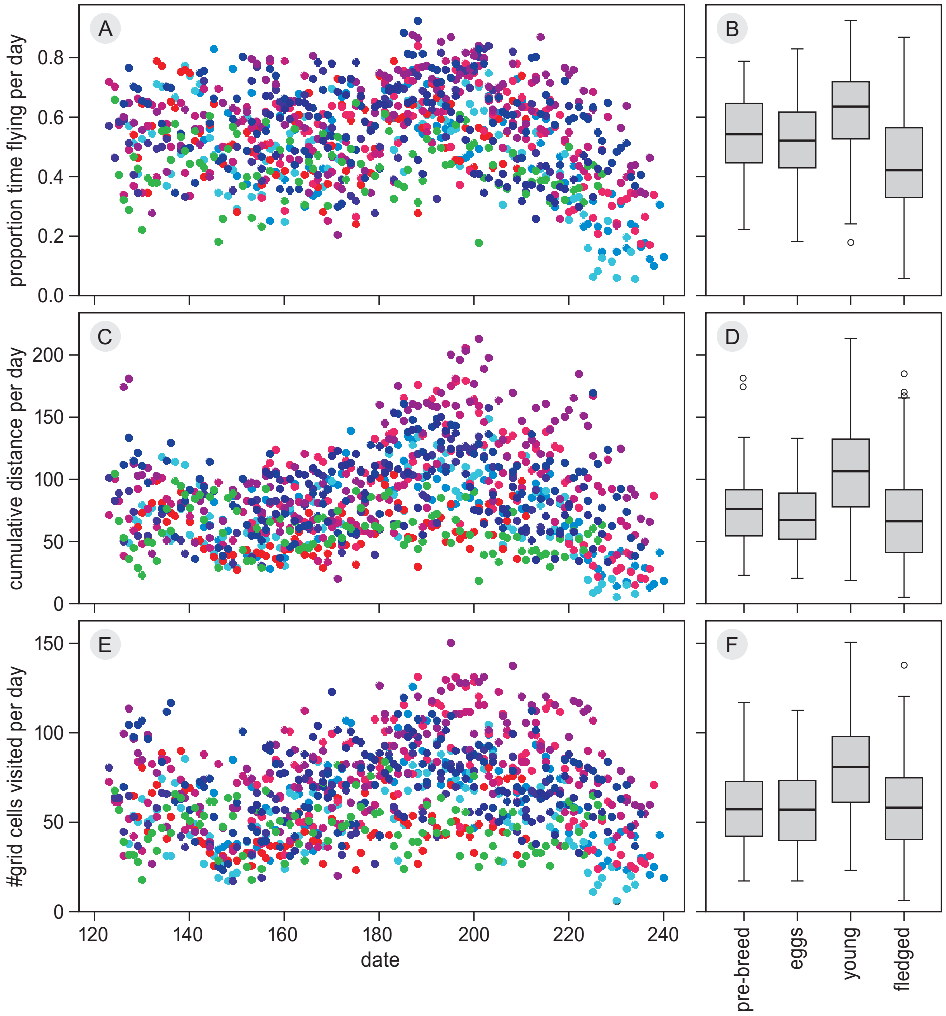

Figure 6.2. Seasonal patterns in proportion of time flying per day (**A/B**), cumulative distance covered per day (**C/D**), and daily home range size (**E/F**). Left panels provide individual daily data points, right panels provide corresponding summaries per breeding phase.

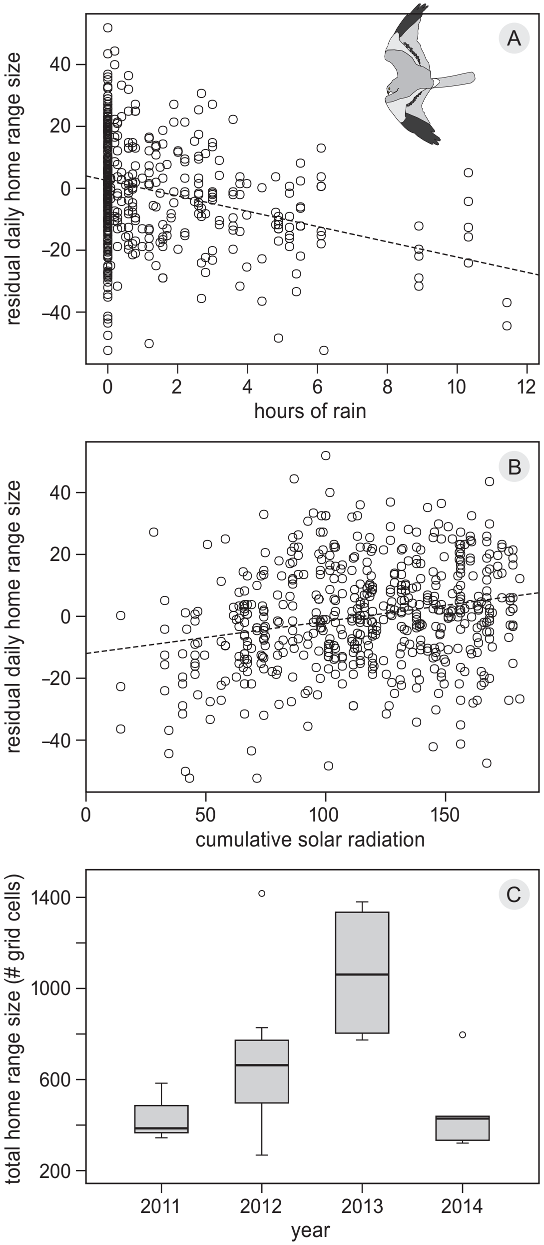

Figure 6.3. (**A/B**) Effect of weather variables (hours of rain per day, cumulative solar radiation per day) on the residuals of daily home range size. Residuals originate from a linear mixed model with season, individual, and year included as random factors. (**C**) Total home range size in different years. Note that a few individuals were tracked in multiple years (Table S1).

$P < 0.001$; $\chi^2_3 = 143.2$, $P < 0.001$). Birds flew most, covered largest distances and occupied largest daily home ranges during the nestling period (Fig. 6.2). Weather had a significant effect on daily activity and home range size, in which birds flew less, covered shorter distances, and used smaller home ranges on days with more hours of rain ($\chi^2_1 = 148.0$, $P < 0.001$; $\chi^2_1 = 85.1$, $P < 0.001$; $\chi^2_1 = 51.9$, $P < 0.001$), and days with lower daily solar radiation ($\chi^2_1 = 117.6$, $P < 0.001$; $\chi^2_1 = 70.2$, $P < 0.001$; $\chi^2_1 = 31.1$, $P < 0.001$; Fig. 6.3A,B).

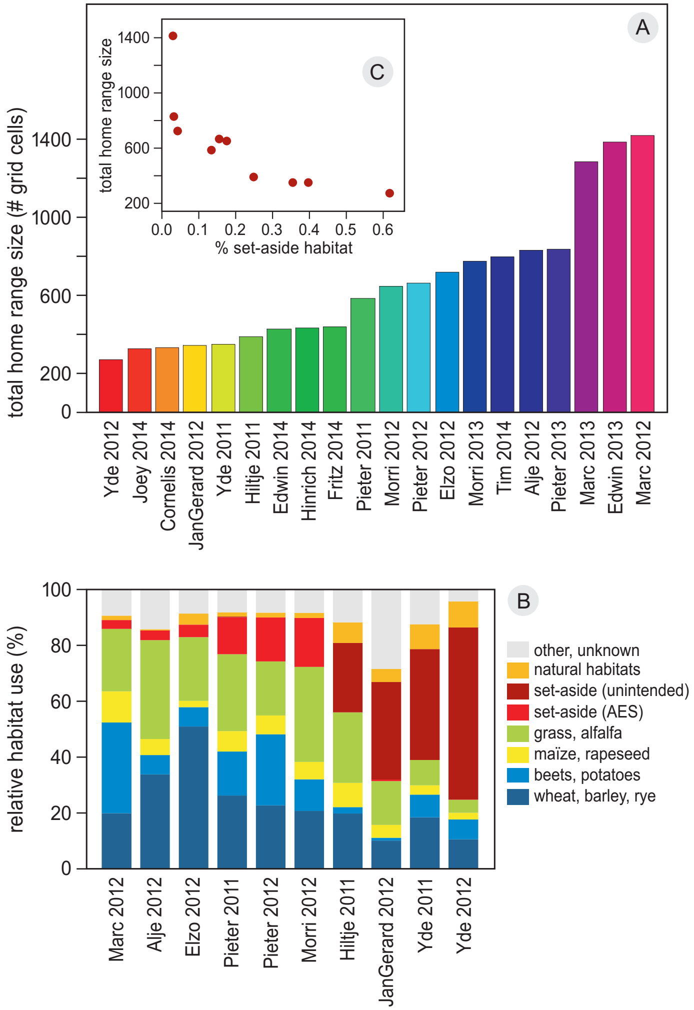

Figure 6.4. (**A**) Total home range size of individual Montagu's Harriers. Seasons are ranked according to home range size. (**B**) Habitat use for the harriers tracked in 2011–2012. (**C**) Inset shows the correlation between the proportion of set-aside in the habitat use and total home range size.

Total home range size differed between years ($\chi^2_3 = 12.1$, $P = 0.007$), in which the harriers had relatively large home ranges in 2012 and 2013 and relatively small home ranges in 2011 and 2014 (Fig. 6.3C). This annual variation in home range size corresponded to annual variation in vole densities; vole numbers were high in 2011 and 2014 (5.0 & 7.9 vole burrows/100 m, respectively) and low in 2012 and 2013 (1.99 & 1.96 vole burrows/100 m, respectively). Furthermore, we found a strong relationship between habitat use and total home range size; the more harriers used set-aside (AES or 'unintended set-aside') the smaller their total home range ($\chi^2_1 = 34.5$, $P < 0.001$, Fig. 6.4B).

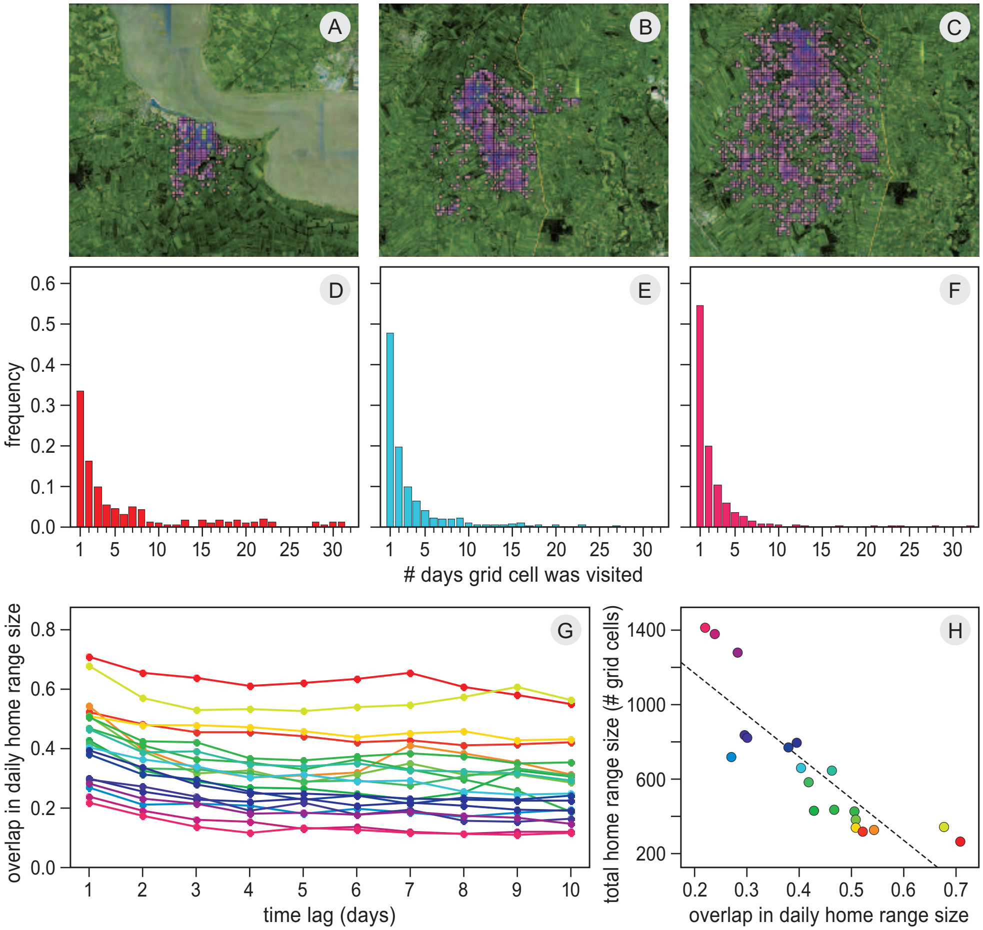

Figure 6.5. (**A-C**) Representative examples of total home ranges of male Montagu's Harriers. Colouration reflects the intensity of use of a square. (**D-F**) Corresponding frequency distributions of the intensity of the use of locations within the home ranges (i.e. use of 250 × 250 m squares). (**G**) Overlap in daily home ranges as a function of time lag. Colours relate to total home range size (cf. Fig. 6.4A). (**H**) Correlation between the overlap in daily home range size (time lag t = 1) and total home range size.

Space use patterns within home ranges

A strong positive correlation existed between the average daily home range size and the total home range size (Fig. S3). However, total home range size varied more than five-fold, whereas daily home range size varied 'only' two-fold between individuals. This discrepancy was caused by a strong negative correlation between total home range size and the degree of overlap between daily home ranges (Fig. 6.5H). Overlap between daily home ranges slightly decreased with an increasing time lag between days (Fig. 6.5G), and was large for individuals with small home ranges and small for individuals with large home ranges (Fig. 6.5G).

These differences were also reflected in the frequency distributions of the number of visits to particular locations (squares) within the home range (Fig. 6.5D-F). Frequency distributions were generally skewed towards few visits, i.e. most squares were visited only a few times. Individuals differed in the amount of squares that were revisited relatively frequently (i.e. the right tail of the frequency distribution). Individuals with relatively small home ranges frequently revisited particular locations within their home ranges more than proportionally. For example, 19% of all the squares that individual 'Yde' visited in 2012 were visited on 10 days or more. In contrast, individuals that occupied very large home ranges seldom revisited locations. For example, only 1% of all squares that individual 'Marc' visited in 2012 were visited on 10 days or more.

Discussion

Factors explaining variation in movement, space use and home range size

We were able to study movements and space use of male Montagu's Harriers in unprecedented detail due to the relatively large amount of accurate GPS-tracking data collected per individual and per day. This revealed that harriers flew most, covered largest distances, and occupied largest home ranges during the nestling phase. These findings corroborate earlier less detailed findings by Trierweiler *et al.* (2010) based on manually radio-tracked Montagu's Harriers, confirming that the nestling period is the most energetically demanding period during the breeding season (Arroyo 1995; Underhill-Day 1993). Seasonal variation in home range size has been reported before in different species (Marquiss & Newton 1981; Saïd *et al.* 2009; Van Beest *et al.* 2011; Börger *et al.* 2006b; Pérez-García *et al.* 2013), but was not found in all cases. For example, for Eagle Owls *Bubo bubo* and Marsh Harriers *Circus aeruginosus*, two other raptor species that are central place foragers during the breeding season, home range size did not vary with breeding stage, indicating more stable space use patterns (Campioni *et al.* 2013; Cardador *et al.* 2009). However, in these studies, seasonal patterns might have been masked by large differences in home ranges between individual birds, or these studies might have lacked the resolution to find subtle differences as only few positions were collected per day.

We also found a clear effect of weather on the behaviour of harriers. One could have expected that harriers intensify foraging activity under adverse weather conditions (rain), given that adverse weather has a negative impact on prey activity and hunting success, but our results suggest the opposite. In accordance with observations from the field that nestlings develop fault bars in their flight feathers during periods of bad weather, the harriers seem to forego hunting and deliver less prey on days with adverse weather (as implied by reduced activity and smaller daily home ranges), which hints on a trade-off between parental investment and offspring condition (Stearns 1992). The positive correlation between daily home range size and daily solar radiation could be explained by harriers exploiting thermals for energy efficient soaring flight on sunny days. Such relationship between soaring conditions and home range size was for example found in Griffon Vultures *Gyps fulvus* (Monsarrat *et al.* 2013).

Total home range size varied between years, which was related to annual variation in the abundance of Common Voles, the preferred prey of Montagu's Harriers in our study area

(Koks *et al.* 2007). Village (1982) found a similar relationship between home range size and vole densities for Kestrels *Falco tinnunculus*. In years with lower vole numbers, harriers feed more on farmland bird passerines such as Yellow Wagtail *Motacilla flava* and Skylark *Alauda arvensis* (Koks *et al.* 2007; Salamolard *et al.* 2000). Wagtails and Skylarks generally occur in lower densities than voles (Greenwood *et al.* 1996; Silva *et al.* 1997), which might explain larger home ranges in years with fewer voles. The latter idea is supported by the observation that Prairie Falcons *Falco mexicanus* increased their home range size when switching from a diet of ground squirrels to a diet of birds and reptiles (Marzluff *et al.* 1997), as well as the general (positive) interspecific relationship between the proportion of birds in the diet of a species and the home-range size of that particular species (Zachariah Peery 2000).

Individuality in behaviour

Tracking studies often highlight (individual) variation in home range size as an unexpected surprising result (Börger *et al.* 2006b; Saïd *et al.* 2009; Van Beest *et al.* 2011; Campioni *et al.* 2013; Cardador *et al.* 2009; Pérez-García *et al.* 2013). However, we should remember that tracking is one of the best methods to highlight that populations consist of individuals, countering the simplified traditional view of the 'average bird'. For example, given the large variation in total home range size of Montagu's Harriers, it is difficult to say what the typical home range size is. We advocate that it is of key importance to embrace (individual) variation in behaviour, and to report variation in behaviour rather than only average values.

It however remains unclear to what extent individual variation in home range size is a characteristic of the individual bird or whether it is dictated by the environment (e.g. reflecting habitat quality). The latter has for example been suggested by Pfeiffer & Meyburg (2015) for the Red Kite *Milvus milvus*, for which they saw an up to 20-fold change in the home range size of the same individual between years. It is difficult to disentangle effects of the landscape (environment) and the individual bird in the Montagu's Harrier as males generally return to almost the exact same field to nest. If we look at the individuals that we tracked in different seasons (n = 5 birds and 11 seasons), we indeed see that individuals generally return to the same nesting site, occupying the same home ranges (Fig. S4), resulting in a significant repeatability in daily home range size between years (R = 0.37 ± 0.179 (SE), P = 0.01; Fig. S5). However, there is one notable exception. Individual 'Edwin' was tracked in 2013 and 2014. In 2014 the bird returned to approximately the same nesting site (distance between the nests in 2013 and 2014 was only 2.5 km), but it occupied a notably different home range (overlap of 0.11 compared to 0.26–0.52 for the other birds). In 2014 the home range was much smaller than the home range used in 2013 (Fig. S4). This illustrates that individual harriers can be flexible in their home range size (i.e. show phenotypic plasticity in space use behaviour), for example as a response to variation in food abundance (note that 2014 was the best vole-year during the study period). It nevertheless remains remarkable that individuals nesting in neighbouring fields in the same year can vary so much in their home range size (e.g. individuals 'Pieter', 'Morri' and 'Marc' that bred within 1500 m of each other in 2012, see Fig. 6.4A), suggesting that the environment is not the only factor dictating home range size but that variation in home range size at least partly reflects systematic differences between individuals.

Different space use strategies

The main advancement of having collected large amounts of tracking data was that it allowed us to also study patterns of space use within home ranges. Relative variation in daily home range size was smaller than relative variation in total home range size, which indicates that total home range size is not simple multiplication of daily home range sizes. Indeed, it seems that individuals with a small home range use the landscape in a very different way compared to individuals with a larger home range, and we suggest that these reflect different space use strategies. Individuals with a small total home range fly less and focus on few sites which they re-visit frequently (Fig. 6.5A-F). As a result, the overlap between daily home ranges is relatively large. In contrast, individuals with a large total home range size fly more and rarely re-visit sites but instead explore new sites every day (Fig. 6.5G,H). Consequently, their overlap in daily home ranges is relatively small. These almost contrasting strategies seem to represent extremes of a continuum of space use strategies in Montagu's Harriers.

We can only speculate about how different home ranges and landscape use strategies arise. Salamolard (1997) suggested that home range size of Montagu's Harriers was related to habitat characteristics of the environment, as he found that home ranges for individuals living in arable land were larger than the home ranges of individuals occupying grasslands (Cardador *et al.* 2009; Salamolard 1997). Interestingly, also in our study, space use strategies seem directly related to habitat use. In particular, the birds with the smallest home ranges, all used large-scale unintended set-aside areas. For example, individual 'Yde' used the dredging depots of the Delfzijl harbour, whereas individual 'Jan-Gerard' used the undeveloped area of the 'Blauwe Stad' housing development project (Wiersma *et al.* 2014). Conversely, the birds with the largest home ranges barely used set-aside habitat at all. For example, individual 'Marc' spent only about 3% of its time hunting on set-aside. These observations suggest a direct link between habitat use and space use strategies (and thus home range size). It should be stressed that it is unlikely that the spatial distribution of foraging habitats dictates space use as birds breeding very close to each other often have very different space use strategies. Instead, the space use strategy and thus home range size seems an intrinsic character of the animal itself.

As the energetic costs of flight are relatively high, individual variation in the proportion of time flying per day reflects important differences in daily energy expenditure. A strategy of visiting many different sites during the day seems to come at the cost of high daily energy expenditure. In fact, the hours flying and cumulative distances covered per day during the nestling period are only marginally shorter than flight times and daily distances during migration periods (Vansteelant *et al.* 2015; Schlaich *et al.* 2017). Daan *et al.* (1996) showed that an (experimentally) enhanced parental effort has a negative effect on parental long-term survival, which makes one wonder why not all harriers have smaller home ranges. A possible advantage of exploring a large number of sites might however be that an individual does not depend on a single specific foraging site; i.e. in the case the main foraging site suddenly becomes unavailable an explorative individual has plenty of alternatives. It would in this respect be interesting to evaluate the performance of individuals for the different landscape use and home range strategies in terms of reproductive success, fitness and survival.

However, an even larger dataset, including more individuals per year would be required to warrant such an analysis.

Advances in tracking technologies will provide the ability to monitor movement and space use at an even higher spatiotemporal resolution in the future. In this paper we have provided an example how tracking the movements of individuals at different scales can provide new insights about basic ecological concepts like the home range size that has been studied already extensively in the past. It is a challenge for the future to integrate information on movement and space use patterns at different spatiotemporal scales as the conceptual and analytical frameworks are still lacking.

Acknowledgements

We thank the farmers for always allowing access on their land and properties. This study would have been impossible without help in the field of countless volunteers, students and the staff of the Dutch Montagu's Harrier Foundation. Christiane Trierweiler helped to fit the first loggers in 2009. Our tracking studies are facilitated by the UvA-BiTS virtual lab (www.UvA-BiTS.nl/virtual-lab), an infrastructure for e-Science developed with support of the NLeSC (http://www.esciencecenter.com/) and Life-Watch, carried out on the Dutch national e-infrastructure with the support of the SURF Foundation. This work was supported by the Ministry of Economic Affairs (EZ), the province of Groningen and Prins Bernhard Cultuurfonds.

Ethics statement

Tracking was licensed by the local ethical committee of the University of Groningen, the Netherlands (permits 5869B and 6429B).

Supplemental material

Overview of sample sizes and additional figures

An overview of the sample sizes (days of tracking data) for the different individuals, seasons and breeding phases is provided. In addition, a number of figures are provided that provide further background information about intra- and inter-individual variation in (daily) home range size, cumulative daily distance, and proportion of daily flight time.

Table S1. Overview of data collected, for different years, individuals and breeding phases. For the different breeding phases, the number of days on which sufficient data was obtained (i.e. more than 100 GPS positions) is given. Breeding phases with too small sample sizes (i.e. less than 10 days) were excluded from the analysis.

Bird ID	Year	Pre-breeding period	Incubation period	Nestling period	Post-fledging period	total # GPS positions
Hiltje	2011	0	0	22	0	3 260
Pieter	2011	0	23	28	0	7 220
Yde	2011	0	8	28	10	7 164
Alje	2012	0	19	31	0	8 059
Elzo	2012	1	27	27	37	13 053
JanGerard	2012	0	0	28	27	9 124
Marc	2012	8	29	32	25	15 785
Morri	2012	0	0	27	35	10 544
Pieter	2012	20	25	27	24	13 743
Yde	2012	11	27	32	12	12 143
Edwin	2013	32	29	32	16	17 449
Marc	2013	15	27	32	25	16 524
Morri	2013	20	29	27	27	16 665
Pieter	2013	20	24	28	5	10 691
Cornelis	2014	0	0	15	0	2 646
Edwin	2014	20	29	32	23	16 747
Fritz	2014	0	0	14	28	7 637
Hinrich	2014	0	0	17	3	3 531
Joey	2014	8	27	28	4	10 474
Tim	2014	0	17	32	27	13 046

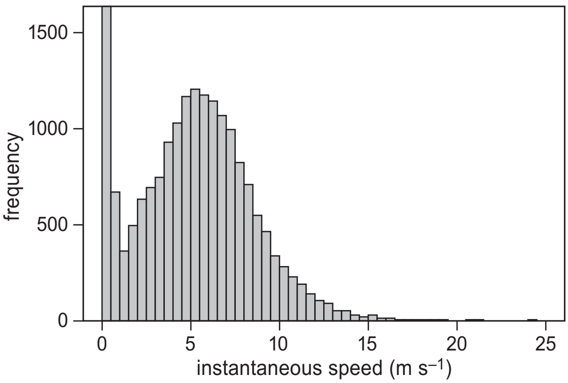

Figure S1. Example of a frequency distribution of instantaneous flight speeds (in m s^{-1}). A threshold of 2 m s^{-1} was used to distinguish between flying and sitting.

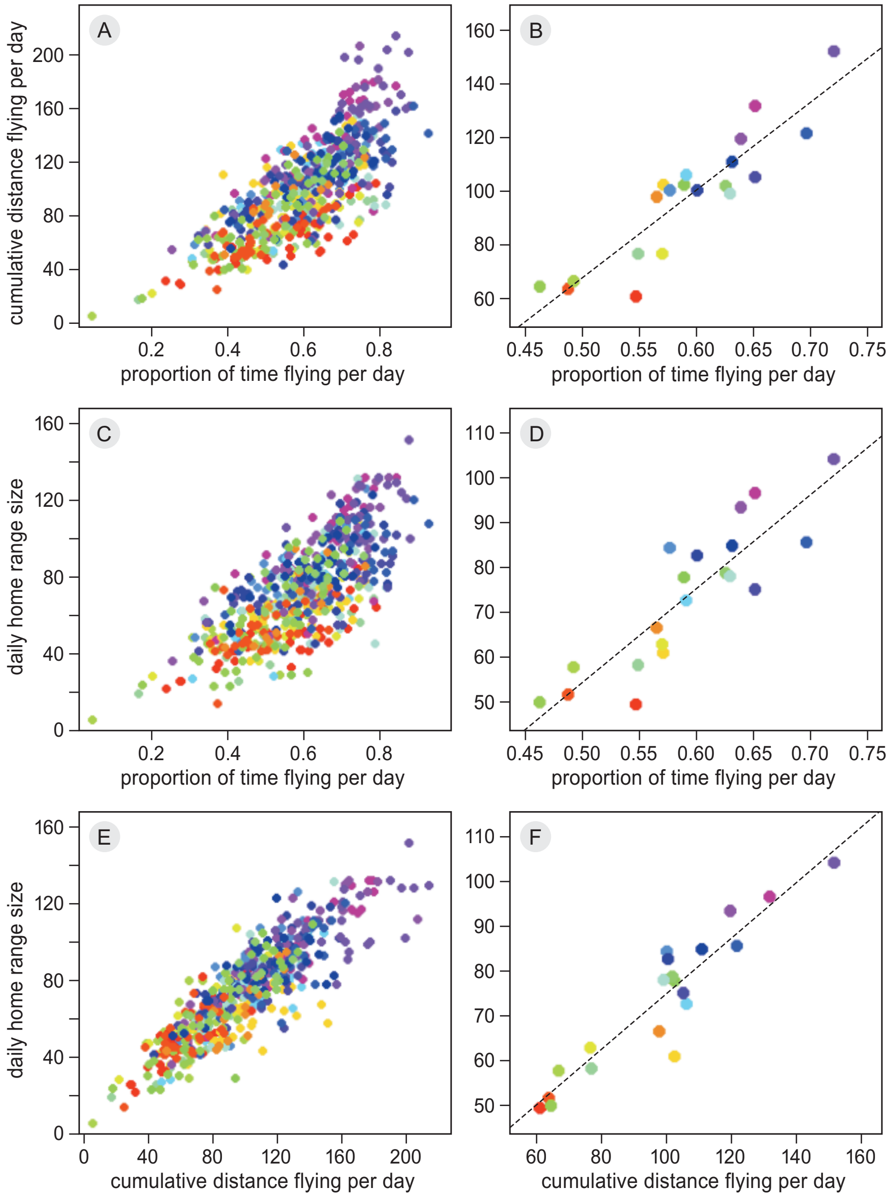

Figure S2. Scatterplots for different behaviours, both within (left column) and between individuals (right column). Behaviours included are proportion of time flying per day, cumulative distance per day and daily home range size.

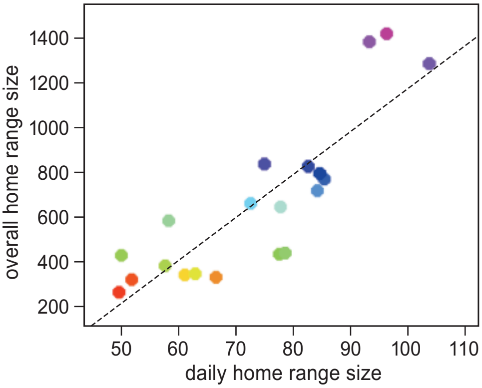

Figure S3. Scatterplot of total home range size against average daily home range size.

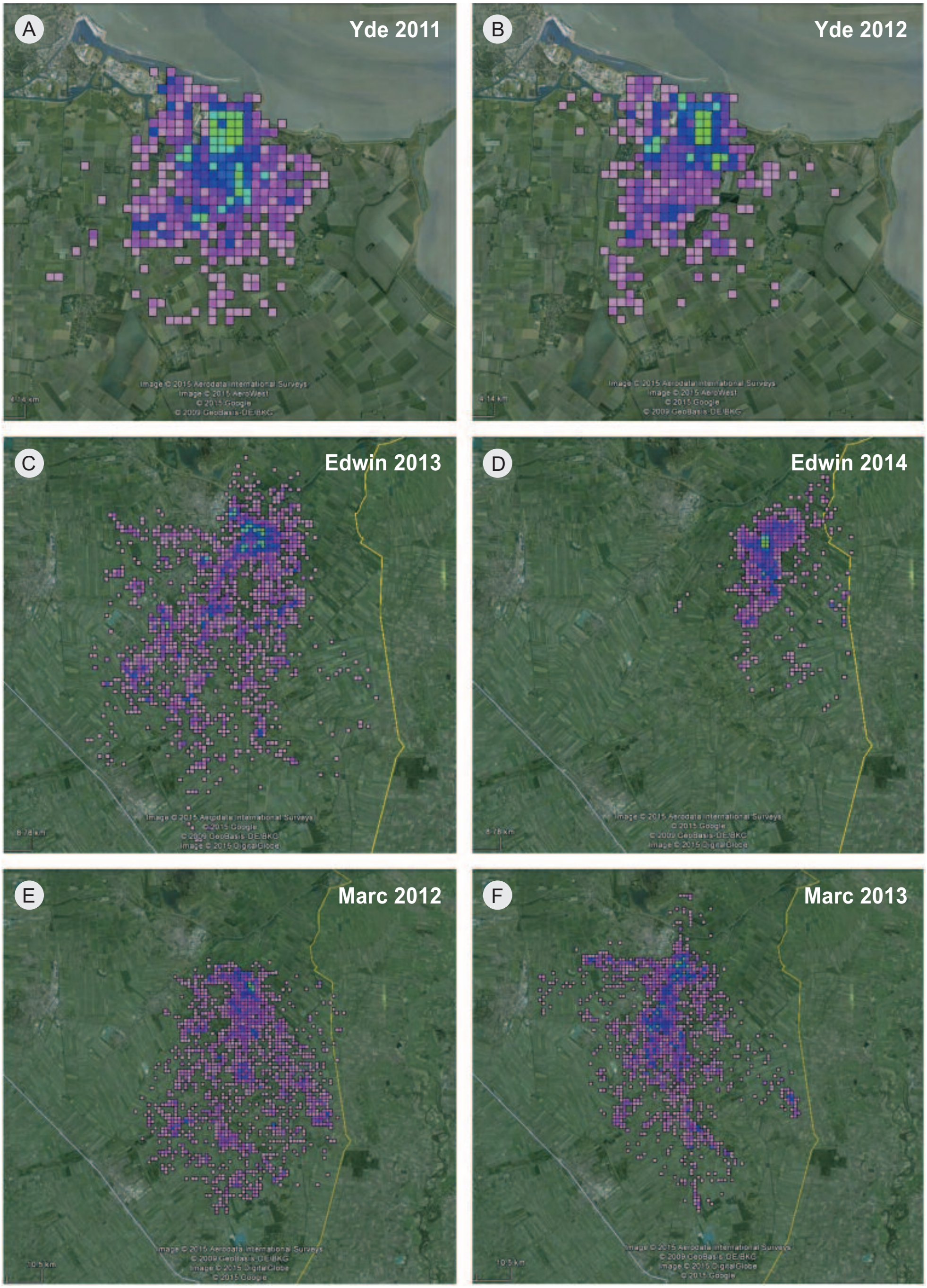

Figure S4. Examples of total home ranges of individuals tracked in more than one breeding season. Colouration corresponds to intensity of the use of the particular square.

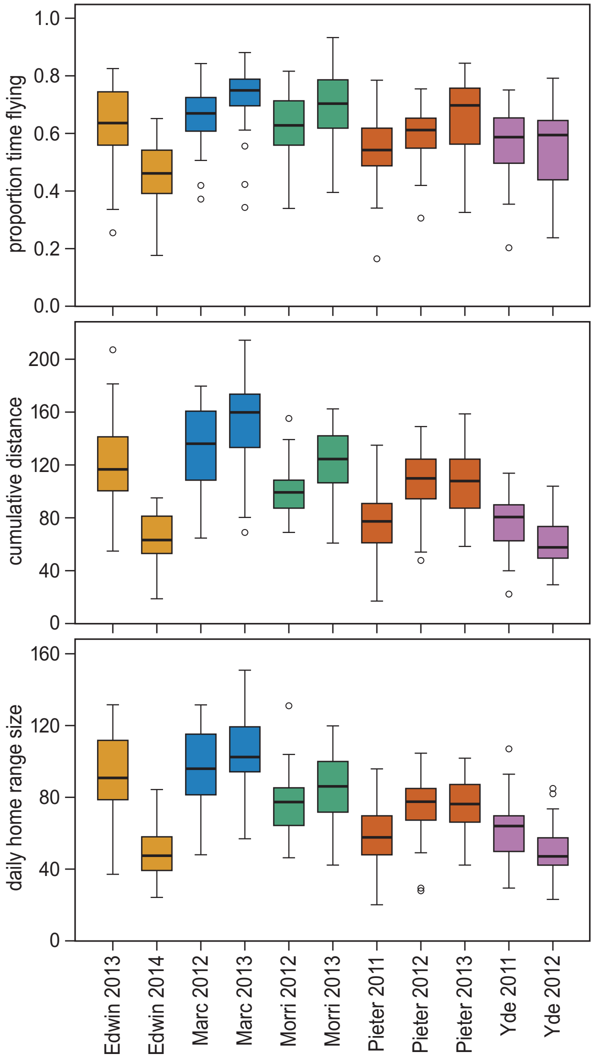

Figure S5. Proportion of time flying per day, cumulative distance per day, and daily home range size for individual male Montagu's Harriers that were tracked during at least two different breeding seasons. Colours refer to different individuals and do not match the colours used in the other figures.

7

Testing a novel agri-environment scheme based on the ecology of the target species, Montagu's Harrier *Circus pygargus*

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Abstract

Farmland birds are in steep decline and agri-environment schemes (AES) to counteract these biodiversity losses are expensive and inefficient. Here we test a novel AES, ‘Birdfields’, designed using detailed ecological knowledge of the target species, Montagu’s Harrier *Circus pygargus*. Current AES, such as field margins, that aim to improve foraging conditions (i.e. vole densities) for harriers are inefficient, as prey are difficult to capture in tall set-aside habitat. ‘Birdfields’ combines strips of set-aside to boost vole numbers and strips of alfalfa, as voles are accessible after alfalfa has been harvested. We found that vole numbers were generally highest in set-aside. Montagu’s Harriers fitted with GPS trackers used ‘Birdfields’ intensively after mowing, preferring mown to unmown strips. Thus, ‘Birdfields’, as a targeted AES for Montagu’s Harriers, is more effective than previous AES due to increased prey accessibility. An additional advantage of ‘Birdfields’ is that it is considerably cheaper, due to the harvest of alfalfa. We advocate that AES should always include monitoring and research activities, aiming at a more adaptive conservation approach.

Introduction

In recent decades, farmland breeding birds have experienced dramatic population declines as a result of the intensification of agricultural practices (Donald *et al.* 2001; Guerrero *et al.* 2012). In Europe, agri-environment schemes (AES) are widely used to counteract biodiversity loss in agricultural ecosystems. However, their effectiveness is often poorly monitored or could not be shown (Kleijn *et al.* 2001, 2004, 2006; Bradbury & Allen 2003; Kleijn & Sutherland 2003). Positive effects are mainly found when AES are targeted to a specific species (Peach *et al.* 2001; Perkins *et al.* 2011; Pywell *et al.* 2012; but see Bright *et al.* 2015). In a world that needs to feed an ever-increasing human population, the high expenses and apparently low effectiveness make current AES unsustainable, calling for cheaper and more effective measures (Vickery *et al.* 2004; Baker *et al.* 2012).

A rare example of a scheme that has led to an increase of the target species' population concerns the Montagu´s Harrier *Circus pygargus* in East Groningen, The Netherlands (Trierweiler 2010). This Red-listed, ground-breeding raptor almost became extinct in The Netherlands at the end of the 1980s (Zijlstra & Hustings 1992). However, a population of nearly 30 breeding pairs established in East Groningen when farmland was set aside on a large scale in the early 1990s (Koks *et al.* 2007). This population further increased after the introduction of AES in 1997 (Koks *et al.* 2007) to around 60 breeding pairs in 2011. In East Groningen, Montagu's Harriers rely greatly on the Common Vole *Microtus arvalis* and both laying date and clutch size are directly related to vole abundance (Koks *et al.* 2007). Moreover, annual population growth rate directly correlates with vole abundance (Koks *et al.* 2007).

The paradox of the successful Montagu's Harrier conservation is that although AES harbour higher vole densities (Koks *et al.* 2007), hunting Harriers capture most prey on intensive grasslands, where prey is less abundant but more accessible directly after mowing events (Trierweiler 2010). Hence, prey availability seems more important than prey abundance alone (e.g. Douglas *et al.* 2009). Based on these observations, we designed a novel AES, coined 'Birdfields', which combines both increased prey abundance and enhanced prey availability. 'Birdfields' consist of alternating strips of set-aside and alfalfa *Medicago sativa* (see Fig. 7.3 and S2). Set-aside consists of a mixture of cereals, grasses and herbs (Wiersma *et al.* 2014, Table S1), and its most important function is to enhance local density of voles. Alfalfa is harvested three times per year, and its main function is to enhance prey availability (i.e. during and directly after mowing). An additional advantage of alfalfa is that it reduces the overall costs of 'Birdfields', making this measure a more economical alternative to current AES (see Discussion).

Here we evaluate 'Birdfields' by describing the ecological determinants of Montagu's Harrier response to this novel AES. This pilot study provides an example of how detailed knowledge of the ecology of the target species has helped to design a more efficient AES for Montagu's Harriers, advocating that ecological research is fundamental to enhance the effectiveness of AES.

Methods

'Birdfields'

Two 'Birdfields' were created in spring 2011 in the Vriescheloërvennen, East Groningen, The Netherlands, close to a core breeding area of the Montagu's Harrier, one at Polderweg (16 ha, 53.09°N 7.12°E) and another at Bisschopsweg (20 ha, 53.09°N 7.11°E, Fig. S1). Half of each field was sown with set-aside and the other half with alternating strips of alfalfa and set-aside (Fig. S2). Birdfields were monitored in subsequent seasons (2012–2013) after the vegetation had fully developed. Alfalfa and, within the context of this particular pilot study, half of the set-aside were mown twice during the harrier breeding season (in 2012 Polderweg was mown on 22 June and 30 July, Bisschopsweg on 12 June and 30 July; in 2013 both fields were mown on 10 June and 25 July). After each mowing, all edges of mown and unmown parts were georeferenced and digitized maps were created in ArcGIS 10.1 (Fig. S2).

Vole abundance

The relative abundance of voles in different crops was estimated by counting vole burrows within 1 m of a 100-m transect line (Franken 2012). Six transects were counted per field, with two transects placed in the middle and four transects within 10 m of the edges of the field. Average field size was 12.4 ha (4.4–17.6, 1st-3rd quantiles, n = 160) in 2012 and 13.9 ha (6.3–18.0, n = 79) in 2013. We did not distinguish between active and inactive vole burrows as a pilot study revealed that even burrows we deemed inactive were used by voles. Counting vole burrows is known to be a relatively inaccurate method (Delattre *et al.* 1990) but it is the only practical method that allows monitoring voles throughout the large home ranges of the Montagu's Harriers. Counts were performed in all common crops in the study area (winter cereals, summer cereals (2012 only), alfalfa, extensive grassland, intensive grassland, rapeseed) and in AES (field margins, set-aside fields, 'Birdfields'). In total, 184 and 89 fields were counted in 2012 and 2013, respectively (Fig. S3).

The relative abundance of voles in set-aside and alfalfa was estimated directly after each mowing event by counting all signs of voles (vole burrows, runways between burrows and small food collection places consisting of pieces of herbs and grasses) in 1-m^2 plots. Plots were counted every 20 m, aligned in the centre of mown strips. In total, 2335 and 3849 plots were counted in 2012 and 2013, respectively. To gain insight on the nature and diversity of potential prey species, all small animals killed or disturbed by the mowing machine were counted during each mowing event, by walking directly behind the mowing machine; 20.6 and 73.3 km were covered in 2012 and 2013, respectively.

Response of Montagu's Harriers

Since 2009, 30 Montagu's Harriers have been equipped with UvA-BiTS GPS trackers (Bouten *et al.* 2013) for ongoing studies on home range size and habitat selection (Klaassen *et al.* 2014). Birds were trapped close to the nest using a mist-net baited with a stuffed raptor. GPS trackers were attached using a 6-mm Teflon harness. In 2012, six male Montagu's Harriers equipped with GPS trackers were breeding within 10 km of the 'Birdfields', of which one's nest failed in the incubation phase. Of the remaining five, four males regularly visited the

'Birdfields' (individuals ID#677, ID#669, ID#704, ID#505). The nest of ID#677 was predated during the incubation period. In 2013, only four birds fitted with a GPS tracker bred within 10 km of the 'Birdfields', three returning birds and one other individual (ID#669, ID#704, ID#505, ID#582). All four visited the 'Birdfields'. The distance between the nests and 'Birdfields' ranged from 2.7 to 5.6 km.

The frequency with which GPS locations are collected can be changed remotely with UvA-BiTS. GPS trackers normally collected GPS positions every 5 min during the day and every hour during the night. At mowing events, GPS trackers collected GPS positions at 3-s intervals ('high resolution measurements') when entering the area of the 'Birdfields'.

For analysis of the general use of 'Birdfields', high-resolution data were subsampled to a 5-min interval. Subsequently, daytime hunting positions were selected, assuming that all positions where the bird was flying were related to hunting. Although these hunting positions include some commuting flights, the proportion of time spent commuting is less than 5%, as commuting flights generally are relatively fast (A.E. Schlaich, R.H.G. Klaassen unpubl. data). The instantaneous speed obtained along with each GPS registration (Bouten *et al.* 2013) was used to distinguish between flying and sitting, using a threshold of 1.2 m s^{-1} (minimum of a two-peaked frequency distribution of speed values). Subsequently we calculated, per day, the percentage of hunting positions on 'Birdfields' relative to the total number of daily hunting positions. To evaluate whether the intensity of the use of 'Birdfields' was affected by mowing, the daily proportion of the use of 'Birdfields' was averaged over three periods: (1) 3 days before mowing, (2) the day of mowing and 2 days thereafter, and (3) 3–5 days after mowing. For this analysis, data for all four mowing events and the two 'Birdfields' were combined.

For analysis of habitat selection of harriers within 'Birdfields', all GPS data, including high-resolution data in period (2) (i.e. 72 h after start of mowing, cf. above), were used. To evaluate whether harriers preferred mown strips over unmown strips and whether they showed a preference for mown alfalfa or mown set-aside, the percentage of positions on mown alfalfa, mown set-aside and unmown set-aside was calculated and compared with the availability of these habitats, as calculated from the digital ArcGIS maps.

Statistical analyses

All analyses were performed in R 2.15.2 (R Core Team 2012). Model selection and validation followed recommendations in Zuur *et al.* (2009).

The mean number of vole burrows per transect in different crops was modelled with a generalized linear model using the R function *glm.nb* in package *MASS* version 7.3-35 (Venables & Ripley 2002). Using the mean of six transects per field, the number of vole burrows per field was explained by fixed effects *year* and *crop type* under a negative binomial distribution (count data with a small mean (12.7) and much larger variance (1059.3), thus with overdispersion). As the model including the interaction term *year* and *crop type* had a higher Akaike information criteria value (1641.7 vs. 1636.5), the interaction term was removed from the final model. A multi-comparison *post-hoc* test was performed to evaluate differences between the crops using R function *testInteractions* from package *phia* version 0.2 (De Rosario-Martinez 2013).

Vole abundance in the different 'Birdfield' habitats was modelled with a generalized linear mixed model using the R package *MCMCglmm* version 2.21 (Hadfield 2010). Because 57% of all observations were zeros, we used a zero-inflated model with a Poisson distribution. Signs of vole activity were modelled as a function of the fixed effects *year* and *habitat*, with *field* and *mowing event* as random effects. The model including the interaction between *year* and *habitat type* had a higher DIC-value (Hadfield 2010), and therefore the interaction term was removed from the final model.

The effect of mowing (periods *before*, *mowing* and *after*) was tested in a generalized linear mixed model using the R function *glmmPQL* in package *MASS*. The average percentage of 'Birdfield' use was modelled as a function of the fixed effect *period*, with *individual* and *year* as random effects with a binomial distribution.

To test if harriers preferred mown strips, a compositional analysis was conducted (Aebischer *et al.* 1993) using the R function *compana* in the *adehabitat* package version 1.8.15 (Calenge 2006). Proportions of surface area (based on digital habitat maps) were averaged per habitat category over the two mowing events and the two 'Birdfields' ('habitat availability'). Proportions of habitat use (based on the number of GPS positions in alfalfa, mown set-aside or unmown set-aside) were averaged per individual over the two mowing events and the two 'Birdfields' ('frequency of habitat use'). Subsequently, frequency of habitat use was compared with habitat availability in the compositional analysis including four birds and three habitat categories. Separate analyses were conducted for the 2 years.

Results

At least five times more vole burrows were found in set-aside habitats compared with all other crops (Fig. 7.1A, Table S2, glmm: difference in deviance 311.97, df = 6, $P < 0.001$, for *post-hoc* test see Table S3). Also within 'Birdfields', there were more signs of vole activity in set-aside than in alfalfa strips (glmm: $P < 0.001$; Fig. 7.1B, Table S4). This emphasizes the importance of set-aside for high prey densities.

By walking behind the mowing machine, a rough impression about the nature and diversity of potential prey species in 'Birdfields' was obtained. In total, 197 small mammals were encountered, 176 Common Voles, six Common Shrews *Sorex araneus*, one Bank Vole *Myodes glareolus* and one Wood Mouse *Apodemus sylvaticus*. Twelve mammals could not be identified. In all, 135 amphibians were recorded: 102 Common Toads *Bufo bufo* and 33 frogs *Rana* sp. Furthermore, two juvenile Common Whitethroats *Sylvia communis* and one juvenile Reed Bunting *Emberiza schoeniclus* were found. In 2013, 62 grasshoppers *Tettigonia viridissima* were encountered. Although amphibians were relatively abundant, they form a negligible fraction of the harrier diet (Koks *et al.* 2007).

Montagu's Harriers fitted with GPS-tracking devices varied greatly in their general use of 'Birdfields' and this variation did not seem to be related to the distance to their nests (Fig. 7.2A, Fig. S4). For example, in 2012, of the three males (ID#669, ID#704, ID#505) breeding at approximately the same distance, only ID#505 used the 'Birdfields' intensively (Fig. 7.2A; ID#677 was a failed breeder). However, mowing had a strong effect on the intensity of the

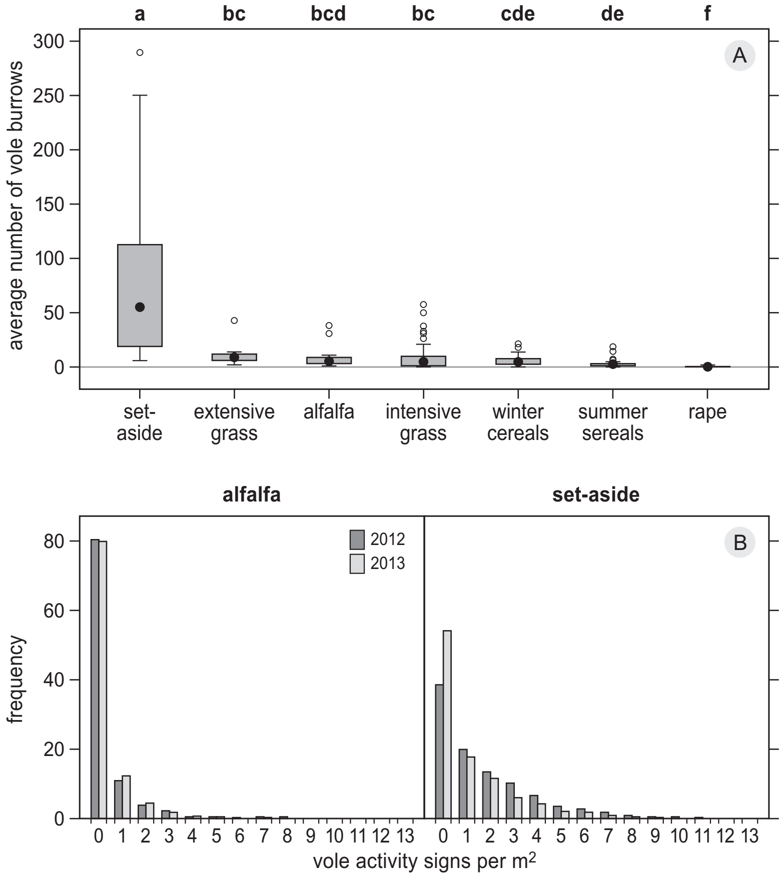


Figure 7.1. (**A**) Average number of vole burrows as counted along 100-m transects in different crops in 2012 and 2013 (n = 272 fields). Boxplots show median (dot), 25th and 75th quantiles (box), extremes (whiskers) and outliers (points). For sample sizes see Table S2. There was no significant difference between the years (glm: difference in deviance 1.12, df = 1, *P* = 0.29). Crop types sharing letters did not differ significantly (**B**) Frequency distribution of signs of activity of voles in 1-m^2 plots (n = 6184) on 'Birdfields' in 2012 and 2013, for alfalfa and set-aside. Less vole activity was recorded in 2013 than in 2012 (glmm: *P* < 0.001; Table S4).

use of 'Birdfields' in all individuals. Harriers visited 'Birdfields' more during and after mowing than before (glmm: t = 5.506, df = 17, *P* < 0.001 and t = 2.204, df = 17, *P* = 0.042, respectively; Fig. 7.2B). In addition, Harriers selected mown set-aside over mown alfalfa, but primarily selected harvested habitats (alfalfa and harvested set-aside) over unmown habitat (unmown set-aside, compositional analysis: in 2012: $\lambda = 0.036$, df = 2, *P* < 0.01; in 2013: $\lambda = 0.075$, df = 2, *P* < 0.01; Figs 7.3 & 7.4).

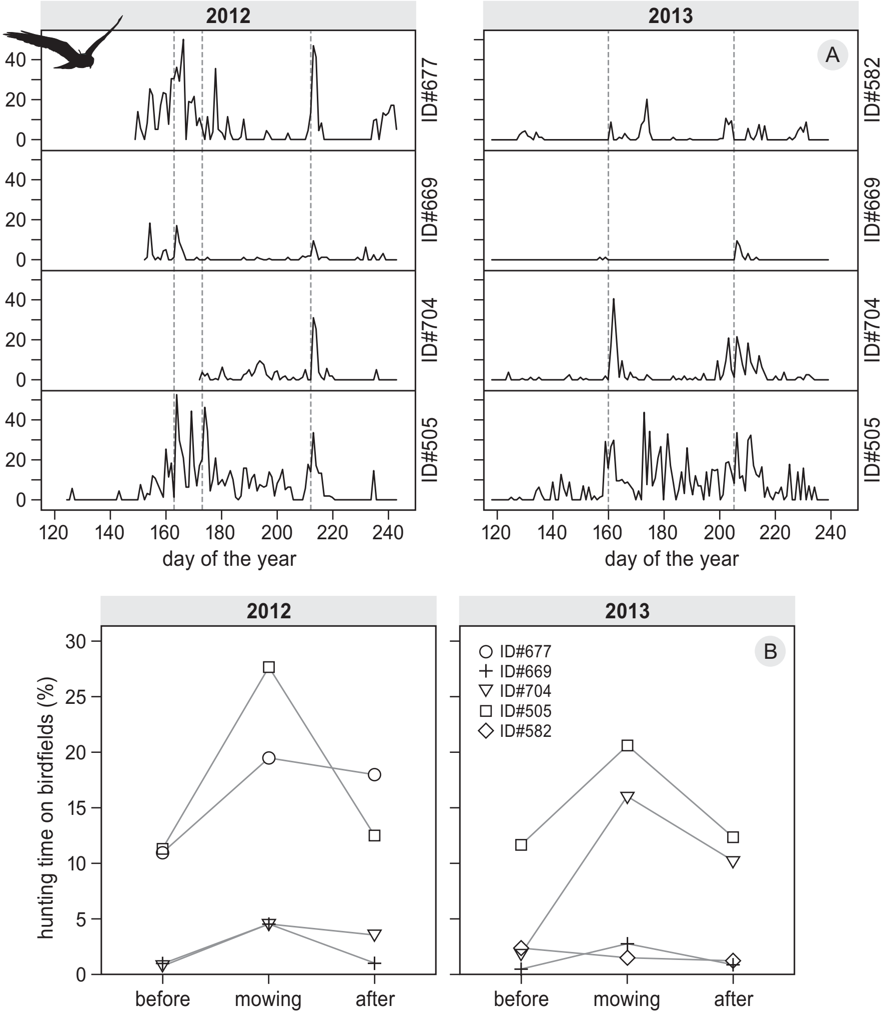


Figure 7.2. (**A**) Use of 'Birdfields' by four male Montagu's Harriers in 2012 and 2013 as percentage of their daily hunting time. Dashed lines indicate mowing events on 'Birdfields'. (**B**) Mean use of 'Birdfields' by male Montagu's Harriers as a percentage of their daily hunting time during the 3 days before mowing, day of mowing and 2 days thereafter, and on 3–5 days after mowing.

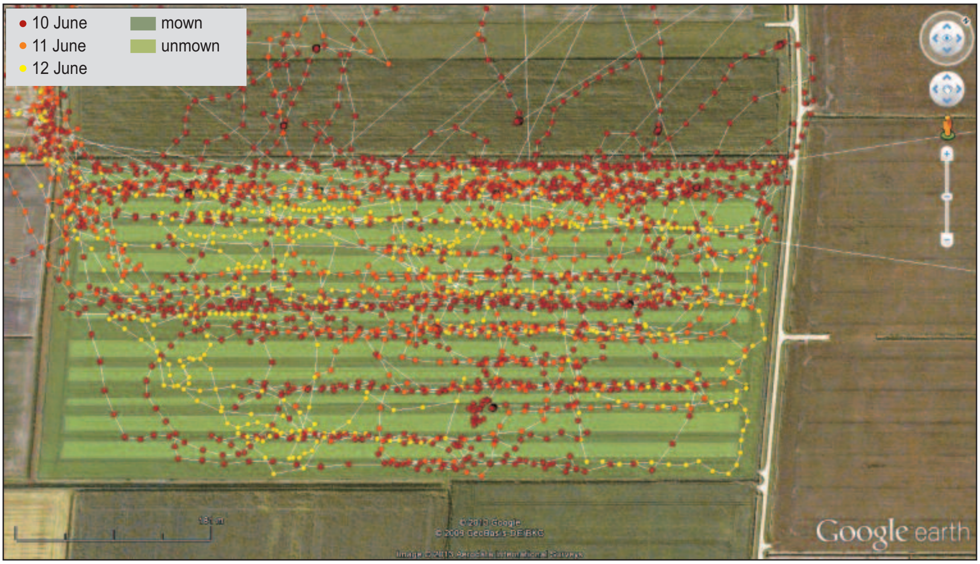


Figure 7.3. Example of the tacks of male Montagu's Harrier ID#704 hunting above a 'Birdfield' on the day of mowing (10 June 2013, red) and the 2 days thereafter (11 and 12 June 2013, orange and yellow). Note that the harrier followed strips of mown habitat.

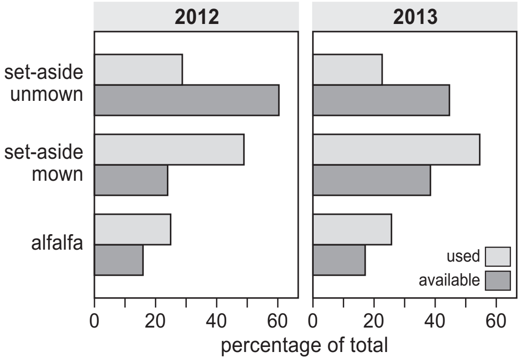


Figure 7.4. Habitat use of Montagu's Harriers hunting on 'Birdfields' compared with habitat availability.

Discussion

Our results suggest that prey availability is more important for habitat selection than prey abundance alone, emphasizing the importance not only of enhancing prey densities but also of making this prey available. This result implies that it is important to measure prey availability (or hunting success) instead of prey abundance when evaluating the efficiency of AES.

The aim of this study was to show that the 'Birdfield' concept works in the sense that harriers immediately respond when voles are made available, rather than quantifying the overall importance of 'Birdfields' for the reproduction or population growth of harriers. The latter would require applying 'Birdfields' at larger spatial scales, comparing individuals breeding in areas with and without 'Birdfields'. This might be difficult as Montagu's Harriers in the Netherlands generally forego breeding in areas without AES. Nevertheless, evaluating the importance of 'Birdfields' for successful reproduction and population growth is an important next step, as we could imagine that 'Birdfields' are most effective in areas where harriers strongly depend on small mammals (e.g. in France: Millon *et al.* 2008; Millon & Bretagnolle 2008) and less effective in regions in which harriers feed mainly on birds (e.g. Terraube & Arroyo 2011).

'Birdfields' were not only favourable for Montagu's Harriers. During the breeding season, other vole-eating species such as Common Buzzard *Buteo buteo*, Common Kestrel *Falco tinnunculus*, Western Marsh Harrier *Circus aeruginosus* and Hen Harrier *Circus cyaneus* regularly visited 'Birdfields' for hunting. Furthermore, substantial numbers of Skylarks *Alauda arvensis*, a species that has heavily declined in our study area (Ottens *et al.* 2013), were nesting in the 'Birdfields'. This is important as Skylarks generally avoid nesting in AES, making it difficult to preserve this species in agricultural landscapes (Kuiper *et al.* 2013, 2015). Other passerines may profit from breeding in set-aside, and thus mowing part of the set-aside during the breeding season is not recommended. Finally, in winter, 'Birdfields' were a magnet for passerines such as finches and buntings, which fed on the cereal-rich set-aside strips, and wintering raptors such as Rough-legged Buzzard *Buteo lagopus* and Hen Harrier.

An important additional advantage of combining set-aside with a harvestable crop is that this makes the measure interesting from an economic point of view, for both the conservationist and the farmer. The current cost to realize 1 ha of set-aside is €2100, which is roughly equal to what a farmer would gain from growing winter wheat. As 'Birdfields' consist of a mixture of set-aside and alfalfa, less is eventually paid per hectare of 'Birdfield'. For example, the current configuration of 'Birdfields' consists of 40% set-aside and 60% alfalfa, so the cost is only €840/ha (2100*0.4). Thus, 'Birdfields' are a cheaper AES than set-aside without alfalfa strips; more hectares of 'Birdfields' can be realized with the same amount of money (in the current example, 2.5 times as much). Alfalfa was harvested and collected by the local crop drier (B.V. Oldambt, Oostwold, The Netherlands) and used for the production of commercial animal food pellets. A farmer normally earns €750/ha from growing alfalfa. It is thus highly advantageous for a farmer to combine alfalfa with set-aside, as the profit from growing set-aside (€2100/ha) more than outweighs the loss of the production of alfalfa (€750/ha), and there might be an additional small financial gain in case part of the set-aside is also harvested (in this particular case, half of the set-aside was harvested during the second alfalfa harvest). Altogether, the farmer earns €1290/ha. It should be stressed that 'Birdfields' are not a profitable alternative to winter wheat (from the perspective of the farmer) as the profit of growing wheat is €2100/ha.

In a world that needs to feed an ever-expanding human population, there will be increasing pressure on biodiversity, and hence the cost efficiency and ecological effectiveness of AES need to be improved. We advocate that AES can be more efficient when measures are designed according to the behaviour and specific ecological requirements of a target species. We have shown that combining areas with high food availability and making these available through common agricultural practices is a promising approach. This is only possible when detailed ecological knowledge of the target species is available, and implementation of AES should therefore always be combined with monitoring and research activities, aiming at a more adaptive conservation approach.

Acknowledgements

We thank the Alfalfa harvesting company *Groenvoederdrogerij Oldambt B.V.* for their collaboration and all farmers in our study area for giving permission to count vole burrows on their fields, especially Z. Krabben-Renken. For help with fieldwork we would like to thank H. Bouman, M. Dijksterhuis, R. Erens, J. Gros, E. Karhausen, P. Kruiger, M. Kuiper, M. v. Laar, M. Meulman, H.J. Ottens, M. Postma, M. Pot, D. Schoppers, S. Van der Sijs, S. Sipma, O. Vlaanderen and P. Wiersma. M. Pot helped with entering the field data. This study was financed by the Ministry of Economic Affairs (EZ), the province of Groningen and Prins Bernhard Cultuurfonds. Our tracking studies are facilitated by the UvA-BiTS virtual lab (www.UvA-BiTS.nl/virtual-lab), an infrastructure for e-Science developed with support of the NLeSC (http://www.esciencecenter.com/) and LifeWatch, carried out on the Dutch national e-infrastructure with support of SURF Foundation. We thank R. Kimball, J. Martínez-Padilla and two anonymous referees for valuable comments on an earlier draft of the manuscript.

Supplemental material

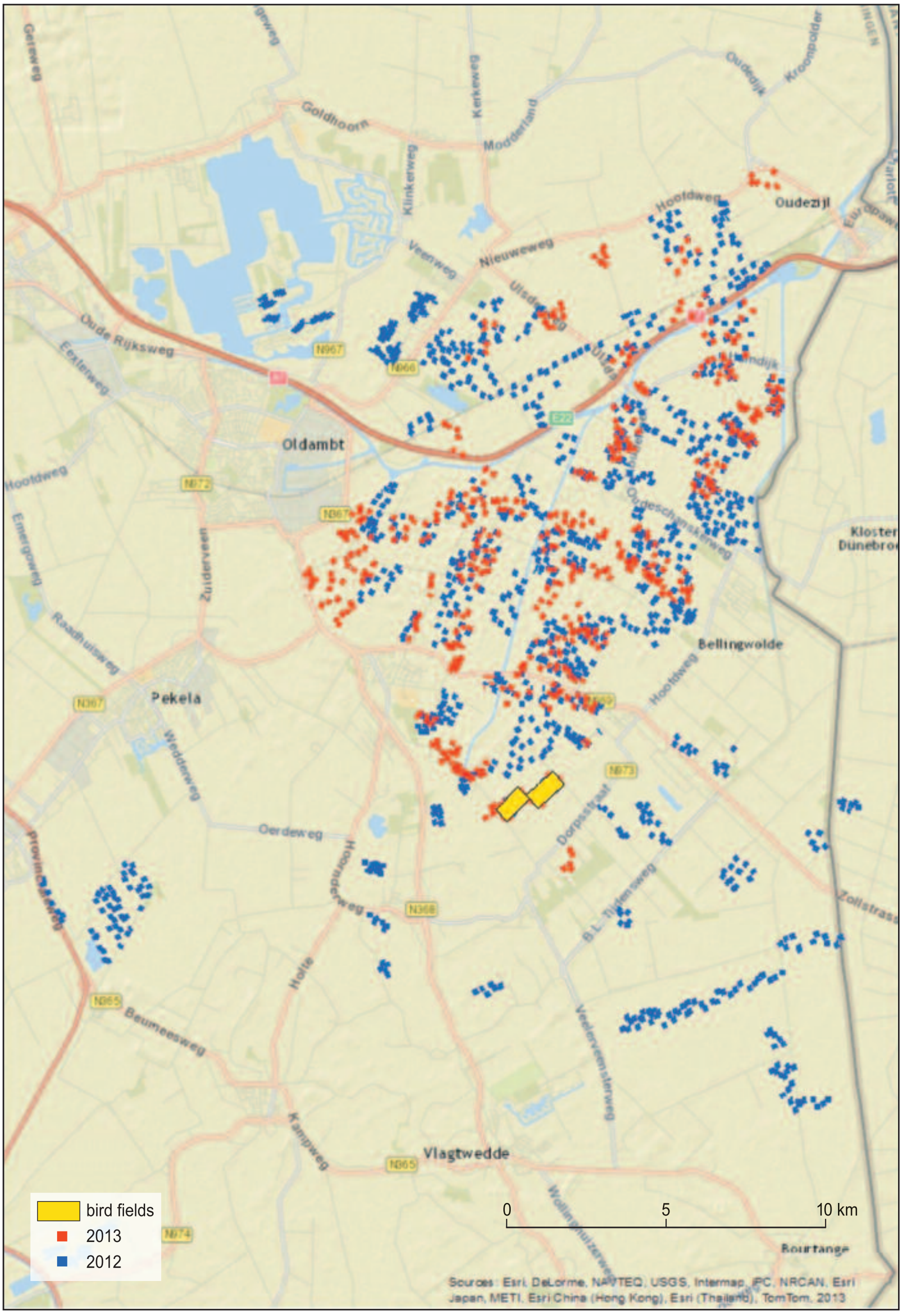
Table S1. Seed mixture for set-aside strips.

Category	Name	Scientific name	%
Herbs	Ox-eye Daisy	*Leucanthemum vulgare*	15
	Bird's-foot Trefoil	*Lotus corniculatus*	14
	St John's Wort	*Hypericum perforatum*	12
	Brown Knapweed	*Centaurea jacea*	10
	Common Yarrow	*Achillea millefolium*	10
	Corn Marigold	*Glebionis segetum*	3
	White Clover	*Trifolium repens*	4
	Red Clover	*Trifolium pratense*	4
Grasses	Timothy-grass	*Phleum pratense*	10
	Vernal Grass	*Anthoxanthum odoratum*	10
	Tall Fescue	*Festuca arundinacea*	4
	Meadow Fescue	*Festuca pratensis*	4
Sum			**100**
Cereals	Oat	*Avena* sp.	20
	Whinter Wheat	*Triticum* sp.	80
Sum			**100**

Of the herbs and grasses 10 kg/ha should be sawn, of the cereals at maximum 25 kg/ha.

Figure S1. Location of the Birdfields within the study area. Map: http://geodata.nationaalgeoregister.nl/top10nl/wms.

Figure S2. Distribution of mown Alfalfa, mown set-aside and unmown set-aside after the first mowing events in 2012 and 2013. Map: http://geodata.nationaalgeoregister.nl/top10nl/wms.



Sources: Esri, DeLorme, NAVTEQ, USGS, Intermap, iPC, NRCAN, Esri Japan, METI, Esri China (Hong Kong), Esri (Thailand), TomTom, 2013

Figure S3. Map of the locations of the vole burrow transect counts throughout East-Groningen. Yellow boxes indicate the location of the Birdfields.

Table S2. Vole abundance (mean number of vole burrows per field counted on six transects of 100 m length) in different crops in 2012 and 2013. Given are median, mean, minimum and maximum values and number of fields sampled (n).

	2012					**2013**				
	Median	Mean	Min	Max	n	Median	Mean	Min	Max	n
Set-aside	63.95	87.56	5.90	289.43	16	38.39	70.41	8.42	250.78	8
Extensive grass	3.85	4.33	1.33	7.81	3	11.08	15.33	5.42	42.49	6
Alfalfa	6.27	9.27	0.83	37.85	10	2.79	6.39	0.20	29.98	9
Intensive grass	4.95	9.02	0	56.76	64	4.57	5.75	0	16.16	38
Winter cereals	4.06	4.80	0.33	20.88	55	2.20	4.44	0	17.71	20
Summer cereals	1.58	2.73	0	17.72	30	-	-	-	-	0
Rape	0.17	0.69	0.14	1.97	5	0.08	0.35	0	1.49	8

Table S3. *P*-values of multiple comparison chi-square tests of the number of vole burrows in different crops.

	Extensive grass	**Alfalfa**	**Intensive grass**	**Winter cereals**	**Summer cereals**	**Rape**
Set-aside	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
Extensive grass		0.490	0.390	**0.030**	**< 0.001**	**< 0.001**
Alfalfa			0.830	0.160	**< 0.010**	**< 0.001**
Intensive grass				**0.010**	**< 0.001**	**< 0.001**
Winter cereals					0.100	**< 0.001**
Summer cereals						**0.010**

Table S4. Number of vole activity signs (vole burrows, runways and food collection places) in one square meter plots on Birdfields in mown Alfalfa strips (left) and mown set-aside strips (right) in 2012 and 2013. Given are mean, minimum and maximum values and number of plots counted (n) separated for the two fields and two mowing events.

			Alfalfa				Set-aside			
			Mean	Min	Max	n	Mean	Min	Max	n
2012	Bisschopsweg	mowing 1	0.34	0	8	131	2.26	0	12	268
		mowing 2	0.61	0	8	148	2.07	0	13	478
	Polderweg	mowing 1	0.13	0	7	214	1.05	0	11	376
		mowing 2	0.52	0	8	218	1.77	0	11	502
2013	Bisschopsweg	mowing 1	0.32	0	8	210	0.83	0	8	558
		mowing 2	0.30	0	5	187	1.32	0	10	730
	Polderweg	mowing 1	0.20	0	5	298	0.93	0	13	780
		mowing 2	0.55	0	11	324	1.44	0	12	762

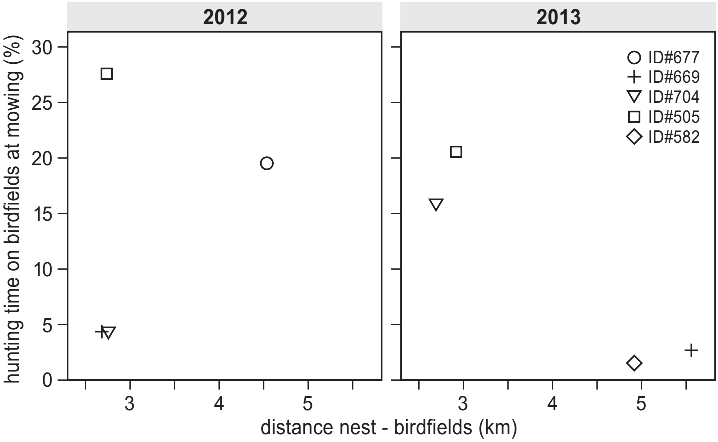
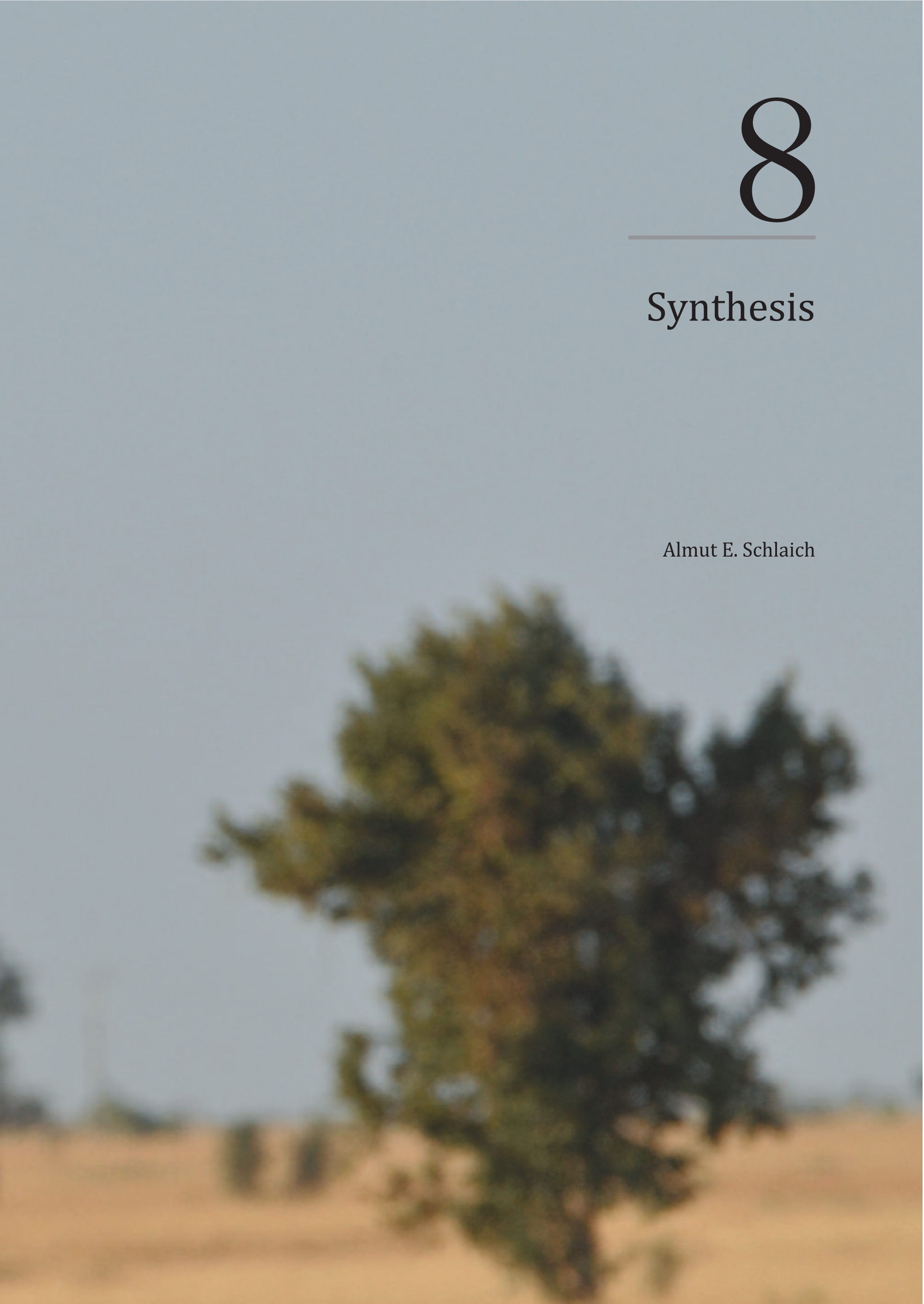


Figure S4. Use of Birdfields by Montagu's Harriers in relation to the distance from their nest.

8

Synthesis

Almut E. Schlaich



Many organisms fail to adjust to the rapid human-made changes of their habitat. This is particularly true for agricultural habitats, and in Europe alone we have lost over 300 million breeding birds during the last century. Long-distance migrants wintering in Africa have also declined during recent decades, and if they rely on agricultural habitats during the breeding season they are in double jeopardy: habitat loss in breeding as well as wintering areas might limit their populations. Conserving biodiversity in agricultural landscapes demands excellent knowledge on the ecological requirements of the species involved. For migratory birds, such knowledge is needed for both breeding and wintering habitats.

The Montagu's Harrier *Circus pygargus* is an extremely good model for understanding how a species is affected by changes on both the breeding and wintering grounds. This species was formerly breeding in natural heathlands, moors and meadows but totally switched to breeding in agricultural habitats over the whole of Europe during the last century, where it still partly depends on natural structures for foraging. As long-distant migrants, Montagu´s Harriers winter in the Sahel, where they use both natural and agricultural habitats. Agricultural practices are changing rapidly in Europe as well as in Africa. Answering fundamental biological questions on the adjustment to different ecological conditions helps to apply successful protection measures not only for a single species but also for a whole ecosystem.

In this thesis, I have investigated how individual harriers cope with the varying environmental conditions they encounter during their entire annual cycle, with special attention to the breeding and the wintering grounds. This individual perspective could be taken because we tracked, together with various collaborators, a large number of harriers from several breeding sites across Europe.

The questions of this thesis were:

How do Montagu´s Harriers use agricultural landscapes in Europe and in Africa? What are the ecological requirements for Montagu's Harriers during the breeding and the wintering season in agricultural landscapes? What is the behavioural response of living in different agricultural landscapes, including possible effects on subsequent migration and breeding events (carry-over effects)?

Results of chapters

In **chapter 2** we give a detailed description of site use throughout the winter in relation to varying annual environmental conditions using a large tracking dataset. Montagu's Harriers were itinerant, using on average three distinct wintering sites to which they showed high site fidelity between years. First sites, used for about one month after arrival, are situated in the northern Sahel and were mainly dominated by natural and sparse vegetation. Intermediate and last sites, being in general further south in the Sahel, were mainly dominated by agricultural and natural habitats. Harriers selected sites with higher habitat diversity compared to random sites. Home range size was largest and activity highest at last sites and higher for individuals wintering in dryer areas. For individuals tracked during multiple seasons, we showed that home range size did not depend on vegetation greenness. However, birds flew more kilometres at the same site in dryer years compared to greener years. The timing of intra-tropical movements was also adjusted to between-year variation in local environmental conditions they experienced, with individuals staying shorter and departing earlier from first sites in dryer years and arriving earlier at last sites in greener years. This demonstrates that individuals have no fixed time schedules but show plastic behaviour in response to environmental conditions which had also been found for stopover duration in Red-backed Shrikes *Lanius collurio* and Thrush Nightingales *Luscinia luscinia* (Tøttrup *et al.* 2012a). The chapter adds to basic knowledge on ecological requirements of the species in winter.

The importance of last wintering sites was further explored in **chapter 3**. Here we show how Montagu's Harriers cope with Moreau's Paradox. Wintering exclusively in the Sahel, harriers find themselves at the southern edge of the Sahelian zone at the last wintering site and have no other option than facing deteriorating environmental conditions as the habitat dries out during the winter. Prey abundance (grasshopper counts which were associated with vegetation greenness) at wintering sites of Montagu's Harriers indeed decreased in the course of the dry wintering period. Harriers responded to this decrease in food availability by steadily increasing their flight time during the second half of the winter. Individuals in areas with stronger declines in Normalized Difference Vegetation Index (NDVI) values increased their flight time more, suggesting that lower food abundance required more intense foraging to achieve energy requirements. The apparent consequence was that Montagu's Harriers departed later in spring when their final wintering site had lower NDVI values and presumably lower food abundance and consequently arrived later at their breeding site. These results indicate that the late wintering period might form a bottleneck during the annual cycle with possible carry-over effects to the breeding season.

Chapter 4 describes the case of an adult GPS-tracked male Montagu's Harrier over-summering in Africa. By relating detailed knowledge of the bird's movements to remotely sensed environmental data (NDVI), we show that over-summering in this case was likely related to an exceptionally difficult breeding season the previous year rather than an effect of adverse weather conditions encountered during the winter or a failed attempt to migrate. This chapter thus provides an example for carry-over effects from the breeding season to subsequent seasons.

After these detailed studies on wintering ecology, **chapter 5** gives a circannual perspective on daily and total flight distances of Montagu's Harriers. GPS-tracks of 29 Montagu's Harriers from breeding areas in France, The Netherlands and Denmark showed that harriers fly between 35,653 and 88,049 km yr^{-1}, of which on average only 28.5% during migration periods. Mean daily distances during migration were 296 km d^{-1} in autumn and 252 km d^{-1} in spring. Surprisingly, males' daily distances during breeding (217 km d^{-1}) were close to those during migration, whereas breeding females moved significantly less (101 km d^{-1}) than males. In terms of daily flight distance, the breeding season seemed nearly as demanding as migration periods for males. During the six winter months, both sexes moved less (114 and 128 km d^{-1} for females and males, respectively) than during migration. Harriers therefore covered shorter daily distances during winter. The winter period thus seems to be the least (energetically) demanding period during the annual cycle, and might act as a buffer to counteract carry-over effects from the breeding season or autumn migration which has also be found in Hudsonian Godwits *Limosa haemastica* (Senner *et al.* 2014) and Collared Flycatchers *Ficedula albicollis* (Briedis *et al.* 2018). However, the example of an over-summering adult male described in **chapter 4** and the possible carry-over effects found in **chapter 3** indicate that this may be a premature conclusion.

Going to the breeding part of the annual cycle, **chapter 6** describes the variation in activity and home range size of male Montagu's Harriers in the main Dutch breeding area. Despite breeding in the same areas, individuals varied five-fold in home range size, reflecting different space use strategies. Individuals with relatively small home ranges moved relatively little and exploited a few high-quality foraging patches which they re-visited frequently. Individuals with relatively large home ranges moved longer distances, rarely re-visited patches but explored new patches instead. Males had smaller home ranges in years with higher prey abundance than in years with low food abundance. This chapter indicates that high-quality foraging habitat is needed to prevent harriers from flying larger distances which otherwise might increase their daily workload to an extent nearly similar to migration days as shown in **chapter 5**.

To improve foraging habitat in the Dutch breeding areas, a novel agri-environmental scheme (AES) for Montagu's Harriers was described and tested in **chapter 7**. Current AES, such as field margins, that aim to improve foraging conditions (i.e. 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 found that vole numbers were generally highest in set-aside. GPS-tracked Montagu's Harriers used Birdfields intensively after mowing, preferring mown to unmown strips. Thus, prey availability appeared more important than prey abundance. Consequently, Birdfields, as a targeted AES for Montagu's Harriers, are more effective than previous AES due to increased prey accessibility. An additional advantage of Birdfields is that it is considerably cheaper, due to the harvest of alfalfa. The new AES described in this chapter offers opportunities to improve foraging habitat for Montagu's Harriers and other vole-eating species in intensive agricultural landscapes.

Discussion of methods used

Throughout the thesis, I used state-of-the-art tracking devices in combination with traditional ecological fieldwork (vole counts, grasshopper counts) and remote sensing data. Tracking birds individually has improved our understanding of bird movements and behaviour considerably. Satellite tracking using 9.5–12 g solar-powered satellite transmitters (PTT-100, Microwave Telemetry Inc.) first allowed to map migration routes and wintering areas of Montagu's Harriers (Trierweiler *et al.* 2013, 2014) as well as mortality patterns during the annual cycle (Klaassen *et al.* 2014). The advent of miniaturized GPS-tracking devices however changed the spatial and temporal scale of movement ecology permanently. We started to use solar-powered UvA-BiTS GPS-trackers in 2009 which enabled us to collect movement data of Montagu's Harriers in unprecedented detail. The greatest advantage of the

UvA-Bird Tracking System is the two-way communication which enables to remotely change the settings of GPS trackers within an antenna-system. This allows to increase the measurement interval in good solar conditions up to one fix every three seconds. The value of such high-resolution measurements has been shown in **chapter 5** where a correction according to GPS interval has been applied to calculate distances covered as close to real values as possible at the moment. The biggest disadvantage of this tracking system is that tagged birds have to be in reach of a local antenna system which means that only birds successfully returning to the same breeding area will add to the dataset on migration and wintering. Birds dying outside the reach of the antenna system or dispersing to other breeding areas upon return are not accounted for. Therefore, we continued using satellite telemetry in addition to our detailed GPS-tracking study.

This great effort lead to an amazing dataset of in total 125 adult Montagu's Harriers from western European breeding populations tracked between 2005 and 2018 using satellite and GPS tags. In total, data on 129 complete wintering seasons were gathered, including 33 individuals that were followed in two or more wintering seasons. This unique dataset allowed us to describe in great detail and with a sufficient sample size how harriers used their wintering sites. The value of this dataset was further improved by combining it with field data in the Dutch breeding area as well as wintering areas in Senegal. Unfortunately, doing fieldwork in Africa is not possible at all relevant wintering sites due to safety and logistic issues. However, a decent sample of data on grasshopper abundance (main food for harriers during the winter) has been collected for two time periods in two winters covering the western part of the harriers' wintering range, which could be used to correlate with remotely sensed data. This made the analyses in **chapter 3** much stronger. It also allowed us to use remote sensing data as proxy for larger scale analyses which we did in **chapters 2 to 4**.

The availability of remote sensing data on a regular basis through space and time gave us the opportunity to investigate the wintering ecology of Montagu's Harriers over the whole of West Africa. However, it should be kept in mind that remotely sensed data has its limitations. The GlobCover land use map is not only limited in temporal resolution, but also in the accuracy and ecological relevance of habitat categories which should be compared to ground-truthed habitats. NDVI is available at a much better spatial and especially temporal resolution, but vegetation greenness cannot explain all (i.e. harriers do not feed on NDVI!) and is not a direct measure of grasshopper abundance. Thus, field data from different areas is necessary to validate the use of such proxies in space and time. Nevertheless, I think that the combination of high-tech tracking devices with data collected in the field and remote sensing data is a valuable approach to add to our understanding of the ecology of the study species (and many other migrant birds). Future developments in tracking devices will further increase the possibilities for researchers to gain detailed knowledge on temporal and spatial movements of birds. It has to be kept in mind however, that individual tracking only sheds light on the individuals followed, and in case of our GPS tags, of individuals that returned to the breeding area. For more in-depth research on population dynamics, large-scale monitoring of harriers in their breeding as well as wintering areas remains necessary. In addition, detailed knowledge, not only on the distribution and movements of harriers, but also on their diet, prey availability and abundance of main and alternative prey items, densities of conspecifics but also of other species preying upon the same food resources is needed. And all this not just on a single spot at a particular time, but rather at the landscape level covered by the focal species and during the entire annual cycle. At the wintering grounds, we actually need to have this ecological information for more than just a single season, because especially in the semi-arid Sahel years are known to vary enormously in rainfall and thus habitat suitability might vary greatly between years. To gather this knowledge, future studies should continue to rely on a combination of methods, following individuals in great detail through high-resolution tracking but also invest in fieldwork to understand the environment of the birds and monitor them at a population level. This requires a large investment in detailed ecological field work in Africa, an effort that is often underappreciated by professional scientists at this time.

Overall conclusions

This thesis enlarged our knowledge on the ecological requirements of Montagu's Harriers during winter and during the breeding season. Based on the combination of fieldwork, tracking of individual birds and remote sensing I sketched the picture of Montagu's Harriers living a quite easy life while in Africa, covering only short daily distances compared to the breeding season or migration periods (chapter 5). However, in the course of the winter harriers increase the time spent flying, daily distance covered and daily home range size (chapter 2). This indicates that circumstances are getting more difficult during winter, in line with Moreau's thoughts from almost half a century ago. Moreover, I showed that in the second half of the winter environmental conditions deteriorate at their last and most important sites (chapter 3). Harriers seem to be able to compensate by working harder, but individuals in dryer areas that work hardest leave latest and arrive latest at their breeding sites (chapter 3). And it must be noted that individuals doing less well, thus having died in winter or on spring migration, were not included in this dataset since only data from birds that successfully returned to the breeding area were collected with the GPS-tracking system. The choice of the wintering area seems thus highly relevant for an individual, because wintering in dryer areas seems to carry over to a later spring departure, an important factor for the apt timing of annual-cycle events including timing of breeding.

The paradox in our long-term work on the annual cycle of Montagu's Harriers is that although I showed that the end of the winter seems not to be an easy period, mortality during the wintering season is generally low (Klaassen *et al.* 2014). Since Klaassen *et al.* (2014) have published their paper, more data on seasonal mortality have been collected through satellite tracking of harriers. In Figure 8.1, I show that the monthly distribution of deaths of 54 satellite-tagged adult individuals is relatively low during the wintering season, and especially peaks during spring migration, which corroborates the previous findings by Klaassen *et al.* (2014) based on data of three *different* raptor species. The remarkably high mortality during spring migration is believed to be related to adverse environmental conditions, in particular headwinds over the Sahara Desert. But it cannot be excluded that part of these birds died because of carry-over effects of harsh conditions and intensified foraging at the

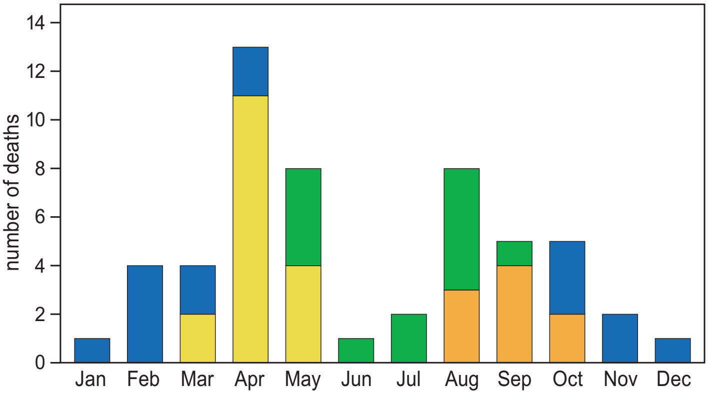


Figure 8.1. Mortality events per month in number of deaths of satellite-tracked adult Montagu's Harriers (n = 54). Colours indicate seasons (blue - winter, yellow - spring migration, green - breeding, orange - autumn migration).

end of the winter. In other words, the main consequence of Moreau's Paradox might be an enhanced mortality during spring migration rather than increased foraging effort or even mortality at the end of the winter itself. The higher number of deaths in February and just before departure in March/April compared to mid-winter (December/January) also hints in the direction of increased mortality at the end of the winter. Unfortunately, our results on increased foraging effort include only birds that successfully returned to the breeding area (GPS trackers) and the mortality data is based on individuals tracked by satellite telemetry, so we cannot make the correlation between how hard birds worked at their last wintering site and the probability of dying during the subsequent spring migration.

Mortality during breeding was found to be a bit higher than during winter (Klaassen *et al.* 2014). This is not surprising keeping in mind that reproduction is a great investment whereas harriers only have to sustain themselves during winter. I showed that especially males cover much larger daily distances during breeding than during winter (chapter 5). This was most pronounced in Dutch males, breeding in a highly intensified agricultural landscape. Dutch birds using high-quality foraging patches fly shorter daily distances and have smaller home ranges (chapter 6). In addition, the introduction of high-quality foraging habitat through the novel AES Birdfields was highly accepted and used by harriers (chapter 7). This indicates that the availability of high-quality foraging habitat might be a limiting factor in this landscape. A striking peak in the number of deaths at the end of the breeding season when food abundance should be highest (harvest of cereals makes voles accessible) also points in this direction. It seems that the consequences of such high investment in breeding are payed within the breeding season with birds dying at the end of the summer and possibly additional carry-over effects to early autumn migration (Fig. 8.1). Klaassen *et al.* (2014) have shown that raptors died mostly in Europe on autumn migration, contrary to spring migration when most birds died during desert crossing. The case of an adult male over-summering in Africa also indicated carry-over effects from the previous breeding season (chapter 4). Improving foraging habitat in the breeding areas seems thus to be very important for the conservation of the species; not only for reproductive success, but also for adult survival and carry-over effects to prevent the breeding season to be the limiting one. These patterns are based on descriptive work only, and causation of the role of landscape features and parental expenditure of subsequent mortality cannot be proven. Experimentation with this species is not practical (and often not desirable because of conservation issues), but comparative work between breeding populations varying in the extent of habitat intensification is a valid way forward to get a better understanding on how landscape features impact on the demography of the species.

Autumn migration seems to be less dangerous than spring migration, showing a much smaller peak in the number of deaths (Fig. 8.1). However, there might be carry-over effects from autumn migration to winter which is indicated by the higher number of deaths in early winter compared to mid-winter.

Re-drawing the graph of total mortality for the four main annual-cycle periods from Klaassen *et al.* (2014) with our now much bigger dataset, I realized that mortality seemed to be higher in winter and during spring migration compared to their paper. This intrigued me and by splitting the dataset into two time periods (birds tagged between 2005–2010 and from 2012–2017) the following picture emerged: total mortality in winter doubled and mortality during spring migration increased 1.5-fold form the first to the second period (Fig. 8.2A/B). The same is true for daily mortality rates (Fig. 8.2 C/D). Daily mortality rates are higher during migration periods, and especially for spring migration. Compared to Klaassen *et al.* (2014), daily mortality rates have increased strongly for winter and spring migration in the second period (Figure 8.2D), resulting in total mortality for these seasons having doubled relative to summer and autumn migration. This results in annual adult survival decreasing from 0.57 for birds tagged before 2011 to 0.43 for birds tagged from 2012 onwards, which might have serious consequences for population dynamics in such a long-lived species. Millon & Bretagnolle (2008) estimated an annual adult survival of 0.67 from 262 birds banded as adults between 1984 and 2004. It has to be kept in mind that our dataset is quite small and no firm conclusions should be made. Nevertheless, this finding is worrying if true.

This apparent increase in winter and spring migration mortality makes me wonder if the situation for Montagu's Harriers is really that leisurely during the winter period as hitherto believed. Even though they only have to sustain themselves during winter, this might have gotten increasingly difficult in recent years. I have shown in chapter 3 that part of the individuals seems to be at sites where they have to work harder, indicating that ecological conditions are difficult, and hence that suitable habitat is limited. Further habitat deterioration due to land-use changes in West Africa might reinforce this effect. Recent observations of "super roosts" with several thousands of Montagu's Harriers might also indicate that many birds have to concentrate in the last remaining high-quality habitats because the surrounding habitats are too deteriorated. In the dry winter of 2014/2015 (see chapter 3), we observed a roost of about 4,000 harriers in Khelcom, Senegal at the same location where a roost of only some hundreds of harriers had been found in the greener winter 2013/2014. At the same time, thousands of Cattle Egrets *Bubulcus ibis*, White Storks *Ciconia Ciconia* and hundreds of Lesser Kestrels *Falco naumannii* were preying on the same food resources (see pictures below). Such big roosts, even though amazing to observe, could be a sign of alarm.

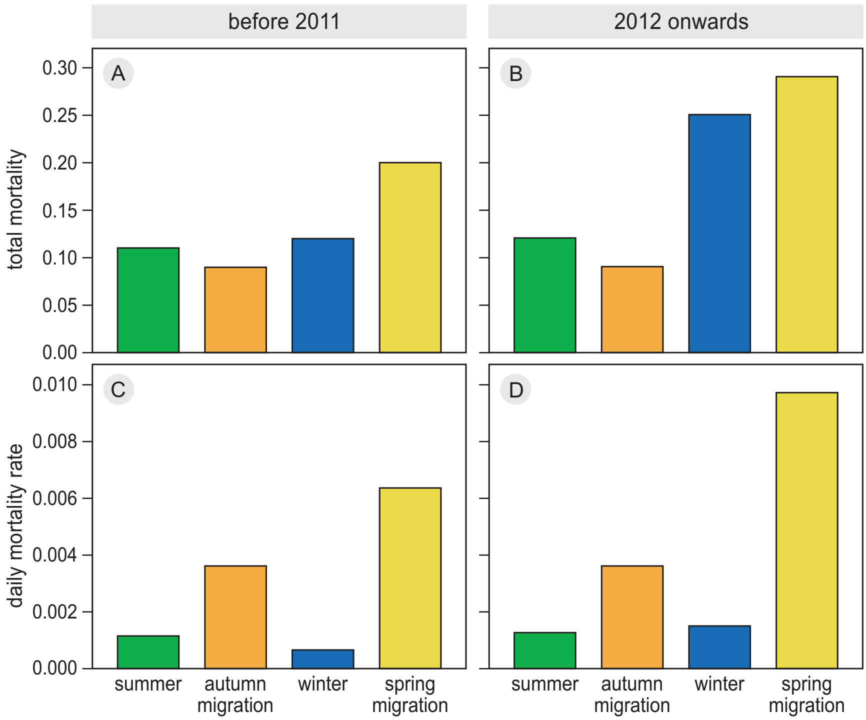


Figure 8.2. (**A/B**) Total mortality and (**C/D**) daily mortality rates during the four main annual cycle periods for adult satellite tracked Montagu's Harriers tagged between 2005 and 2010 (left, n = 31) and adults tagged between 2012 and 2017 (right, n = 23). Total mortality during each period was calculated as 1 – *s* where *s* is the survival during each period calculated as the number of periods survived by the individuals divided by the total number of periods monitored (survival and mortality periods) following Klaassen *et al.* 2014. Daily mortality rates (μ) were calculated from total survival during each period (*s*, from A and B) accounting for the duration of each period (*d*; mean number of days taken from chapter 5; breeding: 101 days, autumn migration: 26, winter: 191, spring migration: 35) according to the formula $\mu = 1 - s^{1/d}$ from Klaassen et al. (2014).

Single sites might form ecological traps, with many harriers relying on them, and their loss could have large-scale population consequences. These developments indicate that although we thought that the main limitation for populations of Montagu's Harries lies in the breeding areas, winter could become or already has become the limiting season.

Lessons for conservation

This thesis contributes to our knowledge on the ecological requirements of Montagu's Harriers. Thus, what did we learn to improve conservation efforts? The finding in chapter 6 that male Montagu's Harriers in an intensive agricultural landscape had smaller home ranges and covered shorter distances in years with higher prey abundance is relevant. This shows that high-quality foraging habitat is necessary to prevent males from having to fly great

Cattle Egrets *Bubulcus ibis* and Lesser Kestrels *Falco naumannii* preying upon grasshoppers in Khelcom, Senegal on 1 February 2015. Photos: Ben J. Koks.

distances to find enough food to provision their young. The fact that Dutch males cover much greater daily distances during the breeding season than French males (chapter 5) indicates that the intensification state of the landscape matters. In the Dutch highly intensified agricultural landscape, it is very likely that high-quality foraging habitat is limited. The Montagu's Harrier population only re-established and increased here thanks to set-aside regulations, the introduction of agri-environment schemes and the active protection of nests (Koks *et al.* 2007). But AES are not available at a large enough scale and vegetation density and height reduce prey accessibility, as shown by the small percentage of AES in habitats that are used by GPS-tracked individuals in chapter 6. This led to an improved AES with prey abundance not just being enhanced, but increasing especially the accessibility of prey. The pilot study on Birdfields and their use by Montagu's Harriers has resulted in the official introduction of Birdfields as an agri-environment scheme within the EU Common Agricultural Policy (CAP). Birdfields are nowadays widely applied in the Netherlands and used to increase foraging habitat not only for Montagu's Harriers, but also for the highly endangered Hen Harrier *Circus cyaneus* and rare Short-eared Owl *Asio flammeus*. They act as islands of high food abundance in the desert-like agricultural area of East-Groningen. To maintain and increase the surface area of high-quality foraging habitat is thus very important, especially in the light of the mortality peak in late summer described above.

Our results add basic knowledge on the ecological requirements of Montagu's Harriers during their stay in the Sahel. Although many of our red-listed species in north-western Europe are wintering in the dry parts of the Sahelian zone, no protection schemes exist in this rapidly changing environment. The surface area of protected areas is small and their protection status in most cases not guaranteed. It has been shown that the decline of Montagu's Harriers, counted during road transects, was less strong in protected areas compared to outside protected areas (Limiñana *et al.* 2012a). However, the fact that there are few protected areas, and that Montagu's Harriers often prefer agricultural habitats results in most of the harriers residing outside protected areas (Limiñana *et al.* 2012a). Ongoing habitat deterioration and destruction due to the ever-increasing human population pressure diminishes the value of protected and unprotected areas ever more in the future. Even though there are some regions that seem to be used by greater numbers of individuals, the vast extent of the wintering range of Montagu's Harriers seems to make the implication of protection measures nearly impossible (Limiñana *et al.* 2012a). The integration of the protection of long-distance migrants as well as African species into sustainable and nature-inclusive agriculture seems to be the only way to keep landscapes with high enough food resources (grasshoppers) without causing great conflicts with humans (crop destruction in agricultural land use) avoiding highly degraded landscapes that are neither beneficial for birds nor for humans.

Future perspectives

Given the findings in this thesis (Fig. 8.3), there are many new avenues we can take to advance our understanding of population dynamics of Montagu's Harriers which may also promote their conservation. Below, I mention several of these avenues that I would have liked to have included in this thesis if time was unrestricted. Data to answer these questions are mostly available and I hope to work on these questions in the near future.

Breeding season

For the breeding season we have shown how Dutch Montagu's Harriers use the space and habitats in their home range in this highly intensified agricultural landscape (chapter 6). It is interesting in itself that the species manages to persist in this landscape, but it would be highly interesting to compare habitat use and home range size with other breeding populations. The Dutch situation seems quite extreme, a very intensive agricultural landscape with nearly no landscape structures. But how much smaller are home ranges in Eastern Poland where parcels are still much smaller and interspersed with natural structures, crop diversity is higher and more alternative prey are available? Bringing together GPS-tracking data and information on ecological determinants (breeding pair density, diet, number of eggs/fledglings) from different European populations breeding in agricultural landscapes varying in intensification stage will be one of the next important steps towards a better understanding of breeding habitat use and its consequences.

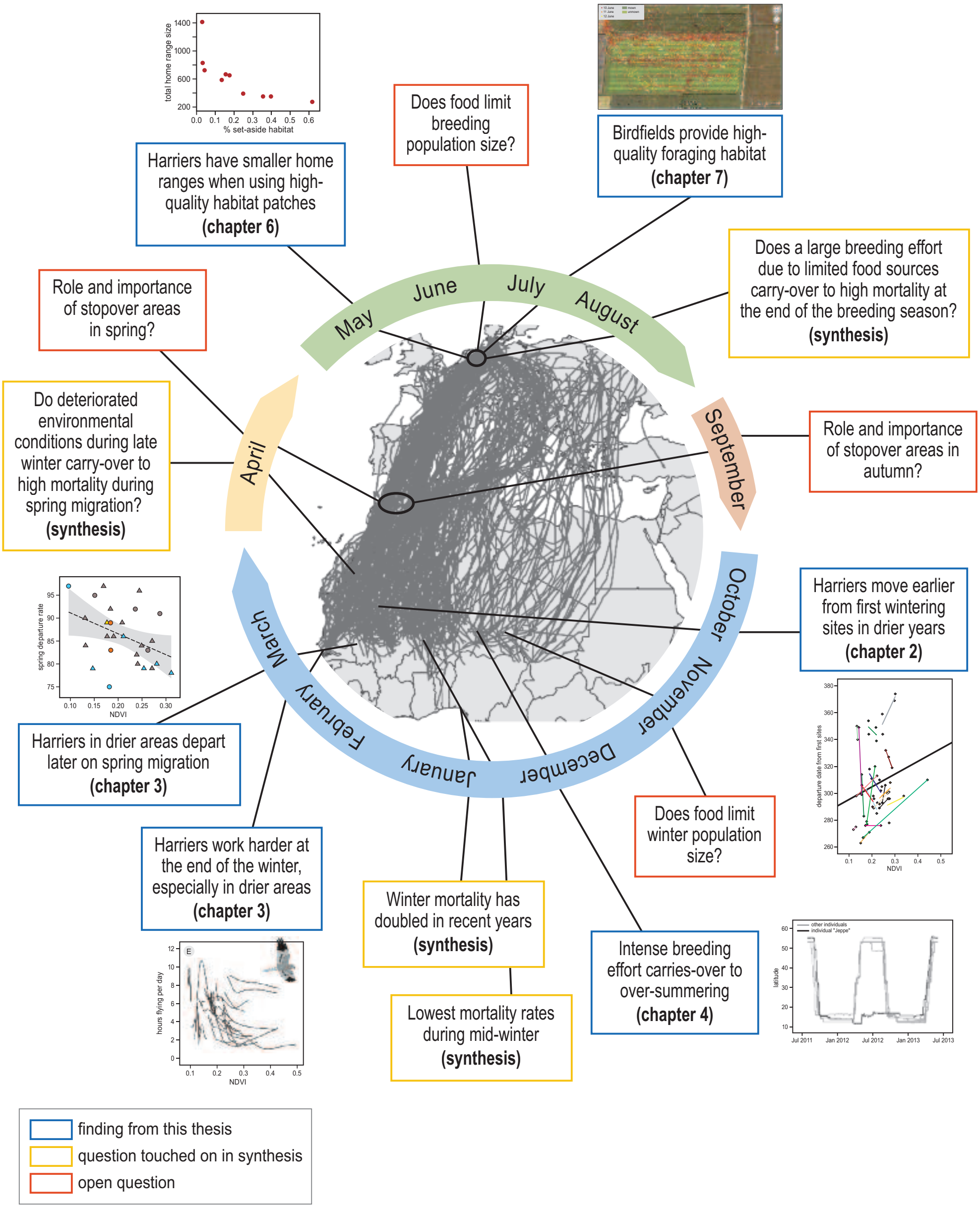


Figure 8.3. Findings from this thesis, questions touched on in this synthesis and open questions around the annual cycle of Montagu's Harriers. Tracks on map show 154 autumn and 119 spring migration routes of 88 Montagu's Harriers followed by satellite telemetry and GPS tracking.

Furthermore, we need to better evaluate to what extent reproductive success depends on local food abundance, thus whether harriers are food-limited during the breeding season. In the breeding area in the Netherlands we created different types and densities of foraging habitat by introducing agri-environmental schemes which could be seen as an experiment on landscape scale. We could try to evaluate the performance of birds living in areas with varying amounts of agri-environmental schemes. Moreover, by mowing experiments we could manipulate instantaneous food availability in the feeding territories of GPS-tracked birds, which will allow us to test ideas about food limitation in intensive agricultural landscapes. This could also be done experimentally by supplying additional food to nestlings to test whether males of supplementary fed nests have to work less hard, and chicks grow into better condition and subsequently survive better and recruit into the breeding population.

Finally, even though we know a lot about the diet of Montagu's Harriers and have some information on food density in different habitats at some places and in some periods, we don't know much about the interaction between these. It is questionable if we ever can retrieve intake rates in different habitats from tracking data, so we need to determine them using field observations during foraging. This should be done throughout the breeding season also covering periods of adverse foraging conditions (bad weather) to determine what they are depending on in such circumstances.

Winter

We have described habitat use at wintering sites of satellite and GPS-tagged harriers during their stay in Africa in chapter 2. For this we used the GlobCover classification of land use, based on remote sensing. However, the accuracy of the GlobCover land-use map and the relevance of its categories for the specific ecological needs of any species is not very straightforward. Detailed analyses of habitat use using high-resolution maps created in the field, also within home ranges, would help to improve our understanding of site selection and possibly help to form ideas for conservation action.

Although we provided indications that food limitation at the end of the winter affects how harriers prepare for migration, we still do not know whether harrier populations are mostly affected by winter or breeding area food supply. To test whether food is limited during winter, we could perform very similar experiments in Africa as we have done with AES in the breeding areas. By manipulating pesticide use, grasshopper abundance could be reduced in large-scale intensive agricultural systems by using bio-pesticides (Mullié & Guèye 2010). By GPS tracking individuals in these and control situations we could determine the direct effect of changes in food abundance on behaviour and habitat use in different landscapes, and evaluate how this may carry over to migration and breeding. Now we have described natural behaviour of the harriers in Africa, it seems the right time for more experimental approaches. As stated earlier on, our knowledge on the main food source of Montagu's Harriers during winter is that they rely on local (non-migrant) grasshopper species (Mullié 2009; Trierweiler & Koks 2009; Mullié & Guèye 2010; Trierweiler *et al.* 2013). However, these studies were based on small sample sizes of pellets collected at few locations. Since then, we collected pellets on roosts ranging from Senegal in the West to Niger in the East, allowing a much better description of the diet composition of Montagu's Harriers on a large spatial scale.

More than 2000 pellets were collected between 2007 and 2015 on roosts in Niger, Burkina Faso, Mali and Senegal. Pellets were collected on roosts and stored individually before being analysed by grasshopper expert Franck Noel in France. If possible, prey remains were identified to species level. A first exploration of part of the dataset has shown that there are notable differences in diet composition between roosts. Analyses will include habitat of the surrounding, prey availability estimates from prey transect counts, and roost size.

As for the breeding season, field observations during foraging in different habitats might give important information on intake rates and thus the value of different habitats. Observing individuals throughout the wintering period, but also at different moments at the same site while the site is deteriorating, could help us to understand how much harder harriers have to work towards the end of the winter. Tracking individuals in high resolution at the same sites might shed light on their space use which can be used in combination with the foraging observations and counts of conspecifics and inter-species competitors at the same place.

Annual-cycle research – carry-over effects

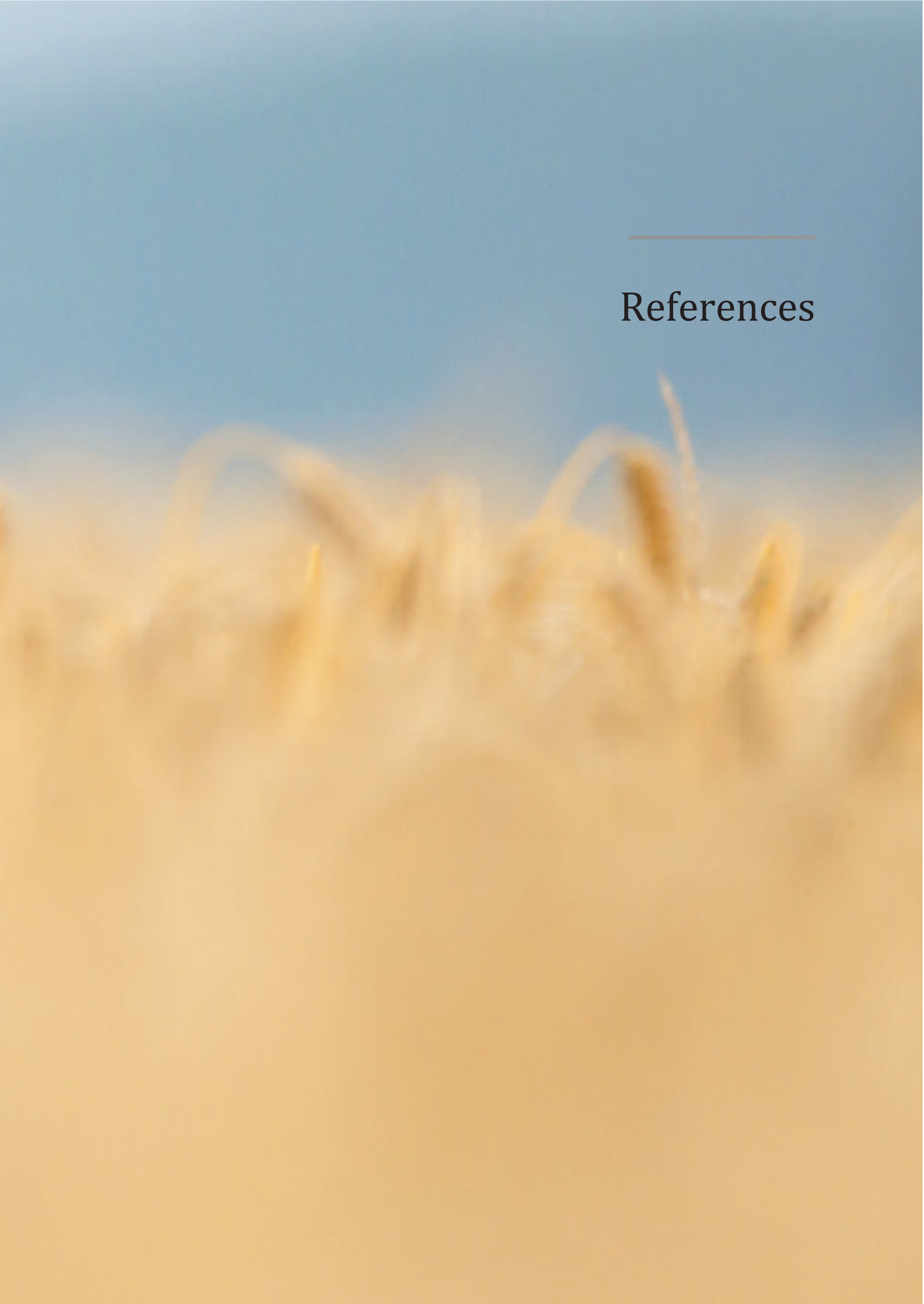
A better integration of ecological processes from winter, migration and the reproductive season is necessary, in which we must understand how conditions at one stage carry over to affect individual performance in subsequent annual-cycle stages. Our dataset used in chapter 2 will allow for within-individual analyses in timing of movements between annual-cycle periods to investigate if and how environmental conditions as well as delays carry over into subsequent seasons. It will also be interesting to investigate how the choice of wintering areas and quality of habitats influences reproductive success and survival. Do birds in dryer areas perform less well? Or do they have a higher chance to die? Do more birds die in dry years when prey availability at the end of the winter is overall less? Or is spring mortality unrelated to wintering conditions and birds die due to extreme weather events like Sahara sand storms? Does e.g. low prey availability have an influence on timing of migration, the length of stopovers, arrival in the breeding area and breeding success? Our existing datasets provide the opportunity to take this next step and answer the above questions which will be a priority in the near future. By analysing these data this way, we will better understand the role of habitat quality on individual performance, and how this may impact population dynamics.

Importance of stopover areas in North Africa

Satellite-tagged Montagu´s Harriers make on average 9-day stopovers in North Africa during spring and autumn migration and individuals that could be followed in consecutive years showed site fidelity to their stopover areas (Schlaich 2011; Trierweiler *et al.* 2014). During four field expeditions to East-Morocco in 2010 and 2011, we observed Montagu´s Harriers during stopover, counted all raptors during road transects, collected data on prey abundance by walking prey transects, and gained insight in food choice by collecting pellets at communal roosts. Montagu´s Harriers preferred farmland and steppe habitats for hunting and therefore chose hunting habitats with higher abundances of potential prey birds. They also avoided heavily degraded habitats which contained less potential prey. The findings of the first field expeditions combined with analyses of satellite telemetry data show that the steppes on the high plateaus of East-Morocco are of great importance for Montagu´s Harriers during stopover in spring as well as in autumn (Schlaich 2011). Overgrazing is threatening this unique landscape and it remains unknown how dependent the harriers are on these stopover areas, and whether they are forming a bottleneck in the annual cycle. Do these areas function as a buffer to make up for delays in departure from the wintering areas or from desert crossing? Could the harriers continue their travels without this important region? Our existing dataset will allow us to deepen our understanding in use and importance of stopover areas.

Ontogeny of migration and finding of wintering areas

This thesis has dealt with how adult Montagu's Harriers manage their annual cycle, with a large focus on the role of wintering habitats. But we know very little on how individual Montagu's Harriers end up at their individual-specific wintering sites in the first place which is important to understand since it determines how we have to distribute conservation efforts. It is one of the biggest remaining open questions in migration ecology in general how juvenile birds learn their migration routes and find their wintering areas and little has been found out till today (Sergio *et al.* 2014; Meyburg *et al.* 2017). As shown in chapter 2, adult Montagu's Harriers are highly site-faithful to their wintering sites, but how do juveniles find these sites? Do they end up there by chance (stochastic juvenile site selection (Cresswell 2014))? Or do they perform vast exploratory movements in their first winter, gaining information on habitat quality by own experience and social information from other harriers? The only way to find out will be to track juvenile Montagu's Harriers and follow their movements not only during their first migration and winter but also in consecutive years. To do this successfully, large numbers of birds must be tracked since first-year survival is especially low (31%, Millon & Bretagnolle 2008). The juveniles should be tracked using satellite telemetry to assure that positions are received also in regions with no GSM coverage like the Sahara Desert and wide parts of Africa. In this way, information on their movements can be gathered, but also on their place and time of mortality. Despite high financial costs, this should nevertheless be one of the priorities for future research.



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Samenvatting

Lange-afstandstrekkers van meerdere kanten bedreigd – de ecologie van de Grauwe Kiekendief jaarrond bestudeerd

We kennen Grauwe Kiekendieven in Nederland tegenwoordig vooral van de grootschalige akkerbouwgebieden in Oost Groningen en Flevoland. Met kunst en vliegwerk wordt een fragiele broedpopulatie hier in stand gehouden. Echter, de Grauwe Kiekendief verblijft slechts vier maanden per jaar in Nederland. De meeste tijd brengen ze door in hun Afrikaanse overwinteringsgebieden. Om de soort te behouden moet je dus eigenlijk ook de omstandigheden en bedreigingen daar kennen. De afgelopen 6 jaar heb ik daarom de ecologie van de Grauwe Kiekendief bestudeerd. In Nederland, maar vooral ook in de Afrikaanse overwinteringsgebieden. Hier worden de belangrijkste bevindingen van mijn proefschrift samengevat.

Eerst wat achtergrondinformatie: populatie-regulatie bij trekvogels

Populatie-regulatie zit bij trekvogels ingewikkeld in elkaar, omdat ze gedurende het jaar van meerdere gebieden gebruik maken. Deze gebieden liggen ver uit elkaar, en verschillen sterk in landschap en omstandigheden (Newton 2008). Een populatie is stabiel als de sterfte tijdens de winter gelijk is aan het broedsucces minus de sterfte tijdens de zomer (Sutherland 1996). Populaties kunnen dan ook door zowel factoren in het broedgebied als factoren in het overwinteringsgebied beperkt worden (Sutherland 1996, Newton 2008). In de jaren 90 van de vorige eeuw werd een verband gelegd tussen de hoeveelheid regenval in de Sahel en de overleving van Grasmussen *Sylvia communis* en Rietzangers *Acrocephalus schoenobaenus* in Engeland (Baillie & Peach 1992). Dit was een duidelijk bewijs voor het idee dat de omstandigheden in het overwinteringsgebied populaties kunnen beperken. Sinds de *Great Drought* (1972–1992) hebben soorten als de Rietzanger en Grasmus zich hersteld. Er lijkt een verschuiving plaats te hebben gevonden van populatie-limitatie in de winter naar populatie-limitatie in het broedgebied (Zwarts *et al.* 2009, Vickery *et al.* 2014, Both *et al.* 2010). Tegenwoordig lijken soorten die zuidelijker overwinteren, in beboste savanne, het juist slechter te doen (Johnston *et al.* 2016). Of dat een populatie gelimiteerd wordt door condities in de overwinteringsgebieden of in de broedgebieden kan dus varieren tussen jaren en habitats (Zwarts *et al.* 2009, Vickery *et al.* 2014, Both *et al.* 2010).

Soms zijn de effecten van verslechtering of verlies aan habitat indirect. Als er bijvoorbeeld door droogte minder voedsel beschikbaar is in het overwinteringsgebied, hoeft dit nog niet te beteken dat er meer vogels dood gaan. Waarschijnlijker is dat de vogels in een mindere conditie aan de terugreis beginnen, waardoor ze ook in mindere conditie of verlaat in de broedgebieden aankomen. Dit resulteert vervolgens in een lager broedsucces. Bij dit soort indirecte effecten spreken we over *carry-over* effecten (Webster & Marra 2005). Het klassieke voorbeeld van een *carry-over* effect betreft de studie van Marra *et al.* (1998) die lieten zien dat Amerikaanse Roodstaarten *Setophaga ruticilla* die in habitat van slechtere kwaliteit overwinterden later in het broedgebied aankwamen en een lager broedsucces hadden. Het feit dat effecten van verslechterde omstandigheden soms indirect zijn, maakt het begrijpen van de populatieregulatie bij lange-afstandstrekkers alleen maar complexer.

Het is meer dan ooit relevant om de populatiedynamica van lange-afstandstrekkers te begrijpen. De afhankelijkheid van meerdere ver uit elkaar gelegen gebieden gedurende het jaar maakt lange-afstandtrekkers namelijk kwetsbaar, getuige het feit dat lange-afstandstrekkers sterker zijn afgenomen dan standvogels en korte-afstandstrekkers (Sanderson *et al.* 2006, Vickery *et al.* 2014). Veranderingen in het landschap en landgebruik in zowel Afrika als ook in Europa spelen hierbij waarschijnlijk een belangrijke rol.

In West Afrika is 90% van de tropische bossen verdwenen, en de overgebleven stukken zijn sterk gefragmenteerd en gedegradeerd (Zwarts *et al.* 2009). Tegelijkertijd is het areaal aan landbouwgrond ten zuiden van de Sahel met 57% gestegen (Brink & Eva 2009). Ook de veedichtheid is enorm toegenomen (Zwarts *et al.* 2009). Deze veranderingen zijn te wijten aan de snelle bevolkingsgroei. Waar er in 2013 zo’n 100 miljoen mensen in de Sahel leefden is de voorspelling dat dit in 2050 tot 340 miljoen gestegen zal zijn (Potts *et al.* 2013). Het kan niet anders dat deze veranderingen invloed hebben op overwinterende trekvogels. Een afname van 83% van gieren en roofvogels in de Sudan zone en de noordelijke Sahel, waarbij het huidige voorkomen vrijwel tot natuurgebieden beperkt is, spreekt wat dat betreft boekdelen (Thiollay 2006a, b, c). Studies naar de ecologie van onze trekvogels in Afrika zijn schaars (Adams *et al.* 2014), terwijl gedetailleerde kennis over het gedrag in relatie tot bijvoorbeeld landschap en landgebruik nodig is om de afnames van lange-afstandtrekkers beter te begrijpen (Vickery *et al.* 2014).

Maar niet alleen de veranderingen in Afrika spelen een rol. Ook in Europa zijn het landschap en landgebruik de laatste decennia sterk veranderd. Door de intensivering van de landbouw is het landschap sterk gehomogeniseerd, wat samen met een intensieve bedrijfsvoering tot biodiversiteitsverlies heeft geleid (Benton *et al.* 2003). Dit wordt misschien nog wel het best geïllustreerd aan de hand van de dramatische afname van de boerenlandvogels (Chamberlain *et al.* 2000, Donald *et al.* 2001, Guerrero *et al.* 2012). Om het biodiversiteitsverlies tegen te gaan werd in 1992 in Europa het agrarisch natuurbeheer geïntroduceerd. Dit heeft echter niet tot biodiversiteitsherstel geleid (Kleijn *et al.* 2001, 2004, 2006, Bradbury & Allen 2003, Kleijn & Sutherland 2003, Pe’er *et al.* 2014).

Dat boerenlandvogels het momenteel zwaar hebben is evident. Ook trekvogels zitten in de hoek waar de klappen vallen. Maar helemaal dramatisch is de situatie voor trekvogels die in landbouwgebieden voorkomen, deze soorten worden van meerdere kanten bedreigd (*double jeopardy*). Inderdaad blijkt dat een groter aandeel soorten trekvogels een afname laat zien voor soorten die in landbouwgebieden broeden (47%) in vergelijking met soorten die elders broeden (23%) (Zwarts *et al.* 2009). Een voorbeeld voor een soort die in deze ongunstige situatie verkeerd is de Grauwe Kiekendief *Circus pygargus*, het onderwerp van mijn proefschrift. Grauwe Kiekendieven worden geconfronteerd met verslechtering en verlies aan habitat door intensivering van de landbouw, zowel in het broedgebied als in het overwinteringsgebied in Afrika.

Het studiesysteem, de Grauwe Kiekendief

De Grauwe Kiekendief komt in Europa ten zuiden van de 60ste breedtegraad vrijwel overal voor. Omvangrijke populaties worden gevonden in Spanje, Frankrijk, Polen en Rusland. Grauwe Kiekendieven overwinteren in Afrika ten zuiden van de Sahara, en in India

(Ferguson-Lees & Christie 2001). De soort staat in veel landen op de Rode Lijst van bedreigde soorten, inclusief Frankrijk, Spanje en Polen (SEO/BirdLife 2010, UICN France *et al.* 2016, Krupiński *et al.* 2015).

In Nederland staat de Grauwe Kiekendief op de Rode lijst als 'ernstig bedreigd' (van Kleunen *et al.* 2017). De soort stond op het punt om uit te sterven toen ze zich ineens spontaan vestigde in Oost Groningen, waar tussen 1988 en 1992 vanwege graanoverschotten grote oppervlaktes aan landbouwgrond uit productie waren genomen (Zijlstra & Hustings 1992, Koks *et al.* 2007). Deze braaklegging bleek de basis voor de huidige populatie van ongeveer 50 broedparen, waarvan het zwaartepunt van de broedverspreiding nog steeds in Oost Groningen ligt.

Van oorsprong broedden Grauwe Kiekendieven in natuurlijke habitats. Ze hebben in Europa echter een opmerkelijke switch naar het broeden in landbouwgewassen gemaakt (vooral wintertarwe, wintergerst en luzerne). Dit heeft deze grondbroeder echter afhankelijk gemaakt van nestbescherming, omdat de jongen veelal niet voor de oogst uitvliegen (Arroyo *et al.* 2002). Daarnaast is voedselbeschikbaarheid in veel gebieden een limiterende factor. Zo is de Nederlandse populatie sterk afhankelijk van het voorkomen van Veldmuizen *Microtus arvalis*. In goede muizenjaren zijn er meer broedparen, die grotere legsels en meer jongen produceren (Koks *et al.* 2007). Deze afhankelijkheid van muizen is het gevolg van lage dichtheden aan alternatieve prooien (met name akkervogels), wat typisch is voor de noordelijke broedpopulaties in Europa (Terraube & Arroyo 2011).

Door Grauwe Kiekendieven uit te rusten met satellietzenders is veel bekend geworden over trekroutes en overwinteringsgebieden. Driekwart van de Nederlandse broedvogels trekt via een westelijke route over Spanje naar de Sahel in West Afrika. De rest volgt een meer oostelijke route via Italië, en deze vogels overwinteren gemiddeld ook wat verder oostelijk in de Sahel. Oost Europese broedvogels volgen bovendien een derde mogelijke route via Griekenland en komen dan ook nog oostelijker in de Sahel uit (Trierweiler *et al.* 2014).

Grauwe Kiekendieven in Afrika

Niet één maar drie overwinteringsgebieden

In Afrika eten Grauwe Kiekendieven vrijwel uitsluitend sprinkhanen (Mullié 2009). Christiane Trierweiler kon op basis van de eerste satellietzenderdata de mythe ontkrachten dat Grauwe Kiekendieven uitbraken van Treksprinkhanen *Locusta migratoria migratorioides* zouden volgen. Tijdens de winter zwerven de kiekendieven niet rond maar bezoeken enkele vaste gebieden waar ze voornamelijk op lokale sprinkhaansoorten foerageren (Mullié 2009, Trierweiler *et al.* 2013). Door zich een paar keer gedurende de winter te verplaatsen, van noord naar zuid, volgen de kiekendieven een "groene gordel" van vegetatie en hoge sprinkhaandichtheden naar het zuiden (Trierweiler *et al.* 2013).

Omdat het zenderen van Grauwe Kiekendieven altijd is doorgegaan, door heel Europa heen, kon ik over een veel grotere dataset beschikken om het habitatgebruik en de bewegingen gedurende de winter te beschrijven (**hoofdstuk 2**). Daarnaast waren er ondertussen vogels met GPS-loggers uitgerust, die veel nauwkeuriger posities geven, wat weer heel andere analyses mogelijk maakt. De Grauwe Kiekendieven bleken gemiddeld drie verschillende plekken gedurende de winter te bezoeken (Fig. 2.1), waarbij individuen tussen jaren zeer trouw aan hun plekken waren. De eerste plekken die de vogels bezoeken, in de noordelijke Sahel gelegen, bleken schaars begroeid met natuurlijke vegetatie. In tweede en derde plekken, zuidelijker in de Sahel gelegen, werd het landgebruik gedomineerd door landbouw. Hierbij selecteerden de kiekendieven plekken met relatief veel variatie in het landgebruik.

Een aantal individuen werd gedurende meerdere winters gevolgd. Dit liet zien dat de kiekendieven het moment van de winterse verplaatsingen aanpassen aan de lokale omstandigheden. In droge jaren verplaatsen de vogels zich namelijk eerder dan in natte jaren (Fig. 2.9). Ze volgen dus niet strikt een interne kalender maar verplaatsen zich als de lokale omstandigheden dusdanig verslechterd zijn dat het beter is om door te reizen naar de volgende plek.

Help, er is steeds minder te eten…

In de winter regent het niet in de Sahel, en dus droogt de Sahel gedurende de winter steeds verder op. De befaamde Britse ornitholoog Reginald Ernest Moreau vroeg zich af hoe de vogels die in de Sahel overwinteren zich kunnen voorbereiden op de voorjaarstrek, inclusief het aanleggen van vetreserves voor de vlucht over de Sahara, als de omstandigheden in het overwinteringsgebied steeds alleen maar slechter worden.

Om dit te onderzoeken reisden we af naar Senegal waar een aantal van onze met GPS-loggers uitgeruste Grauwe Kiekendieven overwinterden. We telden de aantallen sprinkhanen langs vaste transecten, en ontdekten dat de aantallen sprinkhanen tussen januari en maart sterk afnamen (Fig. 3.2). Dus er is inderdaad een probleem voor de kiekendieven; met het uitdrogen van de Sahel neemt het voedselaanbod gedurende de winter af! Hoe hier als kiekendief mee om te gaan? Om die vraag te beantwoorden analyseerden we de GPS-logger data voor het laatste overwinteringsgebied van iedere kiekendief (**hoofdstuk 3**). Het bleek dat de kiekendieven aan het einde van de winter meer gaan vliegen (Fig. 3.4). Kiekendieven zoeken vliegend naar voedsel, oftewel de reactie van de kiekendieven op de daling van het voedselaanbod is om harder te werken (i.e. meer tijd aan voedsel zoeken besteden).

De vraag is of het harder moeten werken gevolgen heeft voor de kiekendieven. Het lukte ons niet om daar inzicht in te krijgen. Wel zagen we dat individuen die relatief slechte laatste overwinteringsgebieden kozen later vertrokken, en daardoor ook later in het broedgebied aankwamen (Fig. 3.5). Omdat broedsucces afhangt van de timing van het broeden, met een beter broedsucces hoe eerder je begint, heeft het verlate vertrek direct gevolgen voor het broedsucces. Het is voor een Grauwe Kiekendief dus cruciaal om een goed laatste overwinteringsgebied te vinden.

De vogel die kwijt was

Eén van de landen waar we Grauwe Kiekendieven gevangen hebben voor het GPS-logger onderzoek is Denemarken. Hier vingen we in 2011 een adulte man die we Jeppe noemden. In 2012 keerde Jeppe niet terug, en we namen aan dat hij dood was (vooral mannen zijn heel erg plaatstrouw en de kans dat we een broedvogel met logger zouden missen is niet heel groot). Echter in 2013 melde zijn logger zich in het voorjaar bij ons antennesysteem. Het bleek dat Jeppe het jaar ervoor helemaal niet naar Europa was gekomen maar in Afrika was gebleven (Fig. 4.2). Dit gaf ons de unieke kans het gedrag van een in Afrika overzomerende kiekendief te bestuderen (**hoofdstuk 4**). Overzomeren van volwassen Grauwe Kiekendieven in Afrika is namelijk extreem zeldzaam. Het was pas de eerste keer dat het gebeurde in het geval van 90 gezenderde vogels.

Jeppe bleek in de zomer in Afrika behoorlijk mobiel, en bezocht de vaste plekken die hij normaliter ook tijdens de winter zou bezoeken, maar ook een flink aantal nieuwe plekken (Fig. 4.1). Hierbij bewoog hij zich ook buiten het gebied waar Grauwe Kiekendieven in de winter normaliter voorkomen. Gezien het feit dat Jeppe in het voorjaar niet eens een poging had gedaan om naar het noorden te trekken suggereren we dat het overzomeren in Afrika een carry-over effect van een extreem druk broedseizoen zou kunnen zijn. Een soort van sabbatical dus. Jeppe had in 2011 inderdaad een extreem zwaar broedseizioen. Hij wist als enige een nest met drie jongen groot te brengen, en dat in een jaar met slecht weer en weinig muizen.

Grauwe Kiekendieven in Europa

Grote en kleine home ranges

In de zomer zijn kiekendieven niet vrij om te gaan en staan waar ze willen, maar zijn ze sterk aan het nest verbonden. Mannen en vrouwen verdelen de taken onderling, waarbij de vrouwen de broedzorg op zich nemen en de mannen voor het voedsel zorgen (Clarke 1996). Hoe de mannen het landschap daarbij precies gebruiken wisten we eigenlijk niet, en dat was de reden om een aantal mannen met een GPS-logger uit te rusten. Met de GPS-loggers konden we de bewegingen van de mannen in groot detail volgen (**hoofdstuk 6**).

Wat ons daarbij direct opviel was de enorme variatie in het gedrag van de individuen. Dit kwam bijvoorbeeld tot uiting in de variatie in de grootte van hun *home ranges* – het gebied dat een mannetje gedurende het broedseizoen bestrijkt (Fig. 6.1). De grootste home range bleek maar liefst vijf maal zo groot als de kleinste home range (Fig. 6.2A). Toen we verder op de data inzoomden bleek dat de vogels met verschillende home range groottes het landschap op geheel verschillende manieren gebruikten. Kiekendieven met kleine home ranges gebruikten dag na dag hetzelfde gebiedje, waar ze dan ook telkens naar terugkeerden. Dit waren grootschalige braakliggende tereinen zoals de baggerdepots bij Delfzijl en de nog niet ontwikkelde Blauwe Stad. Gebieden vol met muizen en andere prooien. Kiekendieven met grote home ranges bezochten iedere dag nieuwe gebieden, en kwamen dan ook zelden op dezelfde plek terug (met uitzondering van het nest natuurlijk). Deze vogels leken veel exploratiever, en foerageerden vooral boven gras (muizen) en wintertarwe (kwikstaarten), en juist vrijwel niet boven maatregelen en braak.

Hoe een individu het landschap gebruikt, en dus ook of dat hij een kleine of grote home range heeft, lijkt echt een eigenschap van het individu, en wordt niet door de omgeving gedicteerd, gegeven het feit dat individuen met kleine en grote home ranges vaak vlak bij elkaar broedden. Het is belangrijk om te beseffen dat de gemiddelde kiekendief niet bestaat, maar dat een populatie bestaat uit individuen die allemaal wat anders doen. Dit is ook een belangrijke notie voor het beleid, want waarschijnlijk werkt variatie in maatregelen beter voor een populatie kiekendieven dan het grootschalig implementeren van één type maatregel. GPS-logger blijken in ieder geval een krachtige tool om de variatie in gedrag en ruimtegebruik van vogels in kaart te brengen.

Maatregelen voor kiekendieven

Een ander belangrijk resultaat van het GPS-loggeronderzoek was dat de Grauwe Kiekendieven de akkerranden nauwelijks gebruikten. Dit is opmerkelijk te noemen omdat akkerranden een maatregel zijn om het voedselaanbod voor kiekendieven te verbeteren, en we weten dat er in de regel hoge dichtheden aan muizen in akkerranden voorkomen. De kiekendieven blijken grasland te prefereren, ook al zijn de dichtheden aan muizen daar lager. Dit leide tot het idee dat de beschikbaarheid van muizen wel eens belangrijker zou kunnen zijn dan de absolute dichtheden. Akkerranden bevatten weliswaar hoge aantallen muizen, maar misschien zijn deze daar door de hoge en dichte vegetatie (te) moeilijk te vangen voor een kiekendief?

Dit bracht ons op het idee van Vogelakkers: een combinatie van stroken luzerne en stroken braakvegetatie. De achterliggende gedachte is dat er door de braakstroken hoge dichtheden aan muizen ontstaan, en dat deze muizen vervolgens makkelijk te vangen zijn net na de luzerneoogst op de luzernestroken.

Om dit idee te testen hebben we bekeken hoe onze 'GPS-loggervogels' de Vogelakkers precies gebruiken (**hoofdstuk 7**). Het bleek dat direct na de luzerneoogst de Vogelakkers als een magneet op kiekendieven werken (Fig. 7.2). Het was ook in het veld indrukwekkend om al die jagende kiekendieven op de Vogelakkers te zien. Zoals verwacht jaagden de kiekendieven vooral boven de gemaaide luzerne stroken terwijl de dichtheden aan muizen in de niet gemaaide braakstroken hoger waren. Vogelakkers lijken dus een goede maatregel voor muizenetende roofvogels zoals de Grauwe Kiekendief te zijn en zijn inmiddels een officiele maatregel in het agrarisch natuurbeheer.

Altijd maar vliegen

Wij mensen zijn altijd onder de indruk van de verre reizen die trekvogels als de Grauwe Kiekendief maken. Echter, Grauwe Kiekendieven zoeken al vliegend naar voedsel, dus ook in de rest van het jaar leggen kiekendieven behoorlijke afstanden af. We vroegen ons af hoeveel kilometer een Grauwe Kiekendief gedurende het jaar in totaal aflegt, en hoeveel daarvan tijdens de trek, zomer en winter. Dankzij de GPS-loggers was dit voor ons een relatief makkelijke vraag om te beantwoorden (**hoofdstuk 5**).

Kiekendieven uit Frankrijk, Nederland en Denemarken vlogen tussen de 35 653 en 88 049 kilometer per jaar, waarvan slechts 28.5% tijdens de trekperioden (Fig. 5.1). De kiekendieven leggen in totaal dus veel meer kilometers af tijdens het broedseizoen en in de winter. Dit komt vooral omdat dit relatief lange perioden zijn (maanden) terwijl de trek relatief kort duurt (weken). Als we kijken naar de gemiddelde afstanden per dag zien we dat de kiekendieven het meest tijdens de trek vliegen (296 km/dag in het najaar en 252 km/dag in het voorjaar), en dat mannetjes gedurende het broedseizoen daar nog verrassend dichtbij komen (217 km/dag – vrouwtjes die natuurlijk ook op het nest zitten leggen gemiddeld 'maar' 101 km/dag af). Verder blijkt dat kiekendieven in de winter de kortste dagelijkse afstanden afleggen (114 km/dag voor vrouwtjes en 128 km/dag voor mannetjes). De winter lijkt voor kiekendieven dus de rustigste periode in het jaar te zijn.

Naar een jaarronde bescherming van de Grauwe Kiekendief – een synthese

De Grauwe Kiekendief is een voorbeeld van een soort die dubbel in de problemen is. Ze zijn kwetsbaar omdat het trekvogels zijn, en dus afhankelijk van meerdere ver van elkaar gelegen gebieden. Daarnaast komen Grauwe Kiekendieven, zowel in de zomer als in de winter, vooral in landbouwgebieden voor, maar door de intensivering van de landbouw verslechtert de kwaliteit van dit leefgebied. Om de Grauwe Kiekendief te kunnen behouden moeten we ze jaarrond beschermen. Kennis over hun ecologie en over de verschillende bedreigingen in broed- en overwinteringsgebieden is daarvoor noodzakelijk.

Verbeteren van het leefgebied in de zomer

Klaassen *et al.* (2014) maakten al eerder een overzicht van waar en wanneer roofvogels inclusief de Grauwe Kiekendief gedurende het jaar sterven. Zij beschreven dat de mortaliteit in de zomer hoger is dan in de winter. Dit is misschien niet zo verwonderlijk als je je bedenkt dat de vogels in de zomer hard moeten werken om hun jongen groot te brengen, terwijl ze in de winter alleen voor zichzelf hoeven te zorgen. Opvallend genoeg stierven de vogels in de zomer vooral aan het einde van de zomer of begin van de herfst. Blijkbaar wordt de prijs voor het harde werken dan betaald.

Ik kon laten zien dat mannen tijdens het broedseizoen veel meer vliegen dan in de winter (hoofdstuk 5). Dit verschil was het grootst voor de Nederlandse mannen, die in de zomer hun kostje bij elkaar moeten zien te scharrelen in het intensieve Groningse boerenland. Mannetjes die hoogkwalitatief foerageerhabitat gebruikten vlogen kortere afstanden en bestreken een kleiner gebied (hoofdstuk 6). Bovendien bleek een nieuwe vorm van agrarisch natuurbeheer, de door ons uitgevonden 'Vogelakkers' als een magneet op jagende kiekendieven te werken (hoofdstuk 7). Dit wijst er op dat de beschikbaarheid van hoogkwalitatief habitat een belangrijke beperkende factor zou kunnen zijn in het Nederlandse intensief gebruikte landschap.

Verbetering van de voedselomstandigheden in Nederland lijkt dus belangrijk te zijn voor de bescherming van de soort, niet alleen voor een goed broedsucces, maar juist ook voor een verbeterede overleving van de volwassen vogels. De aanleg van Vogelakkers is waarschijnlijk een manier om dit te realiseren. Vogelakkers zijn inmiddels een officiele agrarisch natuurbeheer maatregel binnen het Gemeenschappeljk Landbouw Beleid (GLB). In het kielzog van de Grauwe Kiekendief zouden ook andere muizenetende roofvogels van de aanleg van

Vogelakkers kunnen profiteren, met name de nog zeldzamere Blauwe Kiekendief *Circus cyaneus* en de geheimzinnige Velduil *Asio flammeus*.

Verbeteren van het leefgebied in de winter

Gebruik makend van een combinatie van high-tech tracking data, remote sensing, en ouderwets veldwerk schets ik het beeld dat Grauwe Kiekendieven tijdens de winter in Afrika een rustig leven leiden, in ieder geval in vergelijking met de broedtijd (zie boven) (hoofdstuk 5). Maar ook in de winter blijken de kiekendieven het niet altijd makkelijk te hebben. Aan het einde van de winter is de Sahel uitgedroogd, wat een negatief effect heeft op de aantallen sprinkhanen, het stapelvoedsel voor kiekendieven in de winter. De kiekendieven moeten aan het einde van de winter dan ook harder werken om hun kostje bij elkaar te scharrelen (hoofdstuk 3). Reginald Ernest Moreau opperde al een halve eeuw geleden dat de omstandigheden voor trekvogels in de Sahel gedurende de winter verslechteren, en vroeg zich af hoe de vogels hier mee om zouden gaan – een vraag waar wij eindelijk, wat betreft de kiekendieven, antwoord op konden geven.

De paradox in ons langetermijnonderzoek aan de Grauwe Kiekendief is dat hoewel de late winterperiode niet gemakkelijk lijkt te zijn voor Grauwe Kiekendieven, we dan geen verhoogde sterfte zien (Klaassen *et al.* 2014). Wel zien we dat er bovengemiddeld veel vogels dood gaan tijdens de voorjaarstrek, wat voor Grauwe Kiekendieven wat dat betreft een belangrijke *bottleneck* lijkt te zijn. Een deel van die sterfgevallen zouden we kunnen toeschrijven aan slechte weersomstandigheden zoals tegenwind en zandstormen boven de Sahara. Maar we kunnen niet uitsluiten dat de verslechterde omstandigheden aan het einde van de winter hierbij een rol spelen, bijvoorbeeld doordat een vogel zich onvoldoende op de voorjaarstrek heeft kunnen voorbereiden. Oftewel, misschien moeten we de verhoogde sterfte gedurende de voorjaarstrek (deels) als een *carry-over* effect van de verslechterde omstandigheden aan het einde van de winter zien.

Als we het overzicht van waar en wanneer Grauwe Kiekendieven gedurende het jaar sterven opnieuw maken (zie Klaassen *et al.* 2014), maar nu met een veel grotere dataset, zien we een belangrijke verandering. Het blijkt dat de sterfte tijdens de winter en in het voorjaar bijna verdubbeld is (Fig. 8.2). Hier is duidelijk iets veranderd in negatieve zin. Het doet vermoeden dat de grootste bottleneck voor Grauwe Kiekendieven momenteel in Afrika ligt, en dus zou deze periode veel meer aandacht moeten krijgen van natuurbeschermers.

Natuur beschermen in de Sahel is echter geen sinecure. Het oppervlak aan beschermde gebieden is klein en hun staat van bescherming vaak niet gegarandeerd. Alhoewel Grauwe Kiekendieven in beschermde gebieden minder in aantallen achteruit zijn gegaan dan daarbuiten (Thiollay 2006b), is het een feit dat het overgrote deel van de populatie buiten de beschermde gebieden voorkomt, mede ook omdat de kiekendieven landbouwgebieden selecteren (Limiñana *et al.* 2012). Dit geldt eigenlijk voor alle soorten die in de winter in de Sahel voorkomen, inclusief een hele trits aan Nederlandse rode lijst soorten. En het is buiten de natuurgebieden waar momenteel de grote veranderingen in landgebruik plaatsvinden. De imense omvang van de gebieden die belangrijk zijn voor overwinterende trekvogels sluit een aanpak met reservaten uit (Limiñana *et al.* 2012). De enige oplossing is een omslag naar duurzame en natuurinclusieve landbouwsystemen, waarbij mensen en vogels samenleven.

Deze opgave is urgent, gezien de voortgaande verslechtering en vernieling van habitat als gevolg van de steeds groter wordende menselijke bevolkingsdruk, en de aanwijzing dat soorten als de Grauwe Kiekendief daar nu echt problemen door ondervinden. Mede ook door de complexiteit van het vraagstuk betreft dit misschien wel één van de grootste uitdagingen voor de natuurbescherming gedurende de komende decennia.

Summary/Résumé/Zusammenfassung

Summary

Population regulation in long-distance migrants is complex because they use several areas which are widely separated geographically and might differ greatly in carrying capacity. To understand population dynamics and the impact of environmental change on populations, knowledge on reproduction, mortality, dispersal and habitat use as well as their temporal and spatial variation is required. This is of uttermost importance, since long-distance migrant species are in decline, especially species breeding in agricultural landscapes in Europe. The intensification of agriculture has been shown to be the main cause of the dramatic decline of farmland birds in Europe. Species that depend on agricultural landscapes also during their overwintering stay in Africa are in double jeopardy, because rapid and dramatic land use changes degrade and destroy their wintering habitats. To protect these species, in depth knowledge on their ecological requirements during the different annual cycle phases is needed.

Unfortunately, there is still a lack of knowledge on the full annual cycle of many long-distance migrants. The focus of many studies has been on the breeding season and just recently the development of ever smaller tracking devices helps us to gain insight into the remaining annual cycle periods, namely migration and wintering. Still, not all can be seen on the screen and fieldwork on the wintering grounds remains necessary to understand what is happening on the ground. However, doing fieldwork in Africa is often challenging due to difficult logistics and unsafe political situations. Nevertheless, the combination of high-tech tracking data with field observations and remote sensing data is a valuable approach to learn more about the different phases of the annual cycle of long-distance migrants.

In this thesis, I used state-of-the-art tracking devices in combination with traditional ecological fieldwork and remote sensing data to increase our knowledge on the Montagu's Harrier *Circus pygargus*, a long-distance migrant species facing strongly changing agricultural landscapes in the breeding as well as wintering areas. Fieldwork during the breeding season was mostly done in the Netherlands but the dataset could be extended thanks to collaboration with our Danish and French colleagues. During the wintering period, field data was collected in Senegal were many of the north-western breeding Montagu's Harriers spend the winter. 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.

In **chapter 2**, we give a detailed description of site use throughout the winter in relation to varying annual environmental conditions using a large tracking dataset. Montagu's Harriers were itinerant, using on average three distinct wintering sites to which they showed high site fidelity between years. First sites, used for about one month after arrival, are situated in the northern Sahel and were mainly dominated by natural and sparse vegetation. Intermediate and last sites, being in general further south in the Sahel, were mainly dominated by agricultural and natural habitats. Harriers selected sites with higher habitat diversity compared to

random sites. Home range size was largest and activity highest at last sites and higher for individuals wintering in dryer areas. For individuals tracked during multiple seasons, we showed that home range size did not depend on vegetation greenness. However, birds flew more kilometres at the same site in dryer years compared to greener years. The timing of intra-tropical movements was also adjusted to between-year variation in local environmental conditions they experienced, with individuals staying shorter and departing earlier from first sites in dryer years and arriving earlier at last sites in greener years. This demonstrates that individuals have no fixed time schedules, but show plastic behaviour in response to environmental conditions. The chapter adds to basic knowledge on ecological requirements of the species in winter.

The importance of last wintering sites was further explored in **chapter 3**. Here we show how Montagu's Harriers cope with Moreau's Paradox: how all the Palaearctic migrants could (i) sustain themselves in the Sahel and (ii) prepare for spring migration in environmental conditions that are continuously deteriorating during their stay. Wintering exclusively in the Sahel, harriers find themselves at the southern edge of the Sahelian zone at the last wintering site and have no other option than facing deteriorating environmental conditions as the habitat dries out during the winter. Prey abundance (grasshopper counts which were associated with vegetation greenness) at wintering sites of Montagu's Harriers indeed decreased in the course of the dry wintering period. Harriers responded to this decrease in food availability by steadily increasing their flight time during the second half of the winter. Individuals in areas with stronger declines in Normalized Difference Vegetation Index (NDVI) values increased their flight time more, suggesting that lower food abundance required more intense foraging to achieve energy requirements. The apparent consequence was that Montagu's Harriers departed later in spring when their final wintering site had lower NDVI values and presumably lower food abundance and consequently arrived later at their breeding site. These results indicate that the late wintering period might form a bottleneck during the annual cycle with possible carry-over effects to the breeding season.

Chapter 4 describes the case of an adult GPS-tracked male Montagu's Harrier over-summering in Africa. By relating detailed knowledge of the bird's movements to remotely sensed environmental data (NDVI), we show that over-summering in this case was likely related to an exceptionally difficult breeding season the previous year rather than an effect of adverse weather conditions encountered during the winter or a failed attempt to migrate. This chapter thus provides an example for carry-over effects from the breeding season to subsequent seasons.

After these detailed studies on wintering ecology, **chapter 5** gives a circannual perspective on daily and total flight distances of Montagu's Harriers. GPS-tracks of 29 Montagu's Harriers from breeding areas in France, The Netherlands and Denmark showed that harriers fly between 35,653 and 88,049 km yr^{-1}, of which on average only 28.5% during migration periods. Mean daily distances during migration were 296 km d^{-1} in autumn and 252 km d^{-1} in spring. Surprisingly, males' daily distances during breeding (217 km d^{-1}) were close to those during migration, whereas breeding females moved significantly less (101 km d^{-1}) than males. In terms of daily flight distance, the breeding season seemed nearly as demanding as migration periods for males. During the six winter months, both sexes moved less (114 and 128 km d^{-1} for females and males, respectively) than during migration. Harriers therefore covered shorter daily distances during winter. The winter period thus seems to be the least (energetically) demanding period during the annual cycle, and might act as a buffer to counteract carry-over effects from the breeding season or autumn migration. However, the example of an over-summering adult male described in chapter 4 and the possible carry-over effects found in chapter 3 indicate that this may be a premature conclusion.

Going to the breeding part of the annual cycle, **chapter 6** describes the variation in activity and home range size of male Montagu's Harriers in the main Dutch breeding area. Despite breeding in the same areas, individuals varied five-fold in home range size, reflecting different space use strategies. Individuals with relatively small home ranges moved relatively little and exploited a few high-quality foraging patches which they re-visited frequently. Individuals with relatively large home ranges moved longer distances, rarely re-visited patches but explored new patches instead. Males had smaller home ranges in years with higher prey abundance than in years with low food abundance. This chapter indicates that high-quality foraging habitat is needed to prevent harriers from flying larger distances which otherwise might increase their daily workload to an extent nearly similar to migration days as shown in chapter 5.

To improve foraging habitat in the Dutch breeding areas, a novel agri-environmental scheme (AES) for Montagu's Harriers was described and tested in **chapter 7**. Current AES, such as field margins, that aim to improve foraging conditions (i.e. 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 found that vole numbers were generally highest in set-aside. GPS-tracked Montagu's Harriers used Birdfields intensively after mowing, preferring mown to unmown strips. Thus, prey availability appeared more important than prey abundance. Consequently, Birdfields, as a targeted AES for Montagu's Harriers, are more effective than previous AES due to increased prey accessibility. An additional advantage of Birdfields is that it is considerably cheaper, due to the harvest of alfalfa. The new AES described in this chapter offers opportunities to improve foraging habitat for Montagu's Harriers and other vole-eating species in intensive agricultural landscapes.

This thesis enlarged our knowledge on the ecological requirements of Montagu's Harriers during winter and during the breeding season, which can be used to improve conservation measures for Montagu's Harriers. **Chapter 8** summarises and reflects on the findings of the earlier chapters and raises questions for future research. In addition, an update on mortality rates during the four annual-cycle periods hints towards increased mortality in winter and during spring migration in recent years. This could mean that the main consequence of

Moreau's Paradox might be an enhanced mortality during spring migration, rather than increased foraging effort or even mortality at the end of the winter itself. These developments indicate that, although we thought that the main limitation for populations of Montagu's Harries lies in the breeding areas, winter could become or already has become the limiting season.

Résumé

La régulation des populations d’espèces migratrices longue-distance est complexe car ces espèces utilisent plusieurs zones très éloignées géographiquement, et dont la capacité de charge peut varier considérablement. Pour comprendre la dynamique des populations et l'impact des changements environnementaux sur ces populations, des connaissances sur la reproduction, la mortalité, la dispersion et l'utilisation de l'habitat, ainsi que sur leurs variations spatio-temporelles, sont nécessaires. Cela revêt une importance capitale pour ces espèces qui sont en déclin, en particulier celles qui se reproduisent dans les paysages agricoles d’Europe. L'intensification de l'agriculture s'est révélée être la principale cause de la diminution spectaculaire des oiseaux se reproduisant dans ces milieux. Les espèces qui dépendent également des paysages agricoles durant leur séjour hivernal en Afrique courent un double danger, car les changements rapides et spectaculaires dans l'utilisation des sols dégradent et détruisent ces habitats en Afrique. Une connaissance approfondie de leurs exigences écologiques au cours des différentes phases du cycle annuel est nécessaire afin d’assurer leur protection.

Malheureusement, le cycle de la majorité des espèces d’oiseaux migrateurs longue-distance est encore mal connu. De nombreuses études se sont concentrées sur la saison de reproduction et récemment, la mise au point de dispositifs de suivi des déplacements de plus en plus petits nous permet de mieux comprendre les périodes du cycle annuel restantes, à savoir la migration et l’hivernage. Bien que le travail de terrain en Afrique soit souvent difficile, en raison des contraintes logistiques et des situations politiques dangereuses, il demeure nécessaire pour comprendre ce qui se passe sur ces zones. En effet cela permet de pouvoir combiner les données de suivi des déplacements par balises avec des observations de terrain et des données de télédétection, ce qui constitue est une approche précieuse pour en apprendre davantage sur les différentes phases du cycle annuel des migrateurs longue distance.

Dans cette thèse, j'ai utilisé des dispositifs de repérage à la pointe de la technologie, combinés à des travaux de terrain en écologie et à des données de télédétection, pour approfondir nos connaissances sur le Busard cendré *Circus pygargus*, une espèce migratrice longue-distance confrontée à des paysages agricoles en pleine mutation aussi bien en période de reproduction que dans ses quartiers d’hiver. Les travaux de terrain pendant la saison de reproduction ont été effectués principalement aux Pays-Bas, mais le jeu de données a pu être étendu grâce aux collaborations avec nos collègues danois et français. Au cours de la période d’hivernage, des données de terrain ont été collectées au Sénégal puisqu’un grand nombre des Busards cendrés qui se reproduisent en Europe de l’Ouest y séjournent en hiver. Sachant que les Busards cendrés passent la moitié de leur cycle annuel dans leurs aires d’hivernage africaines et que les conditions d’hivernage peuvent influencer leurs populations par leurs effets de survie et de report, cette thèse part d’une perspective africaine.

Dans le **chapitre 2**, nous décrivons en détails la manière dont les sites sont utilisés tout au long de l'hiver, en fonction des diverses conditions environnementales annuelles et à l'aide d'un vaste ensemble de données de suivi télémétrique. Pendant l'hiver, les Busards cendrés étaient mobiles, utilisant en moyenne trois sites d'hivernage distincts, auxquels ils montraient une grande fidélité interannuelle. Les premiers sites, utilisés pendant environ un mois après leur arrivée, étaient localisés dans le nord du Sahel et étaient principalement constitués par une végétation naturelle et clairsemée. Les sites intermédiaires et finaux, généralement situés plus au sud, étaient dominés par des habitats agricoles et naturels. Les Busards ont sélectionné des sites présentant une diversité d'habitat plus élevée que des sites choisis aléatoirement. La taille du domaine vital était plus grande, et l'activité plus élevée, sur les derniers sites, et plus élevée pour les individus hivernant dans des zones plus sèches. Pour les individus suivis pendant plusieurs saisons, nous avons montré que la taille de leur domaine vital ne dépendait pas de la verdure de la végétation. Cependant, les oiseaux ont parcouru plus de kilomètres sur le même site les années sèches par rapport aux années plus humides. Le calendrier des mouvements intratropicaux a également été ajusté à la variation interannuelle des conditions environnementales locales rencontrées, les individus restant moins longtemps et partant plus tôt des premiers sites les années sèches, et arrivant plus tôt sur les derniers sites les années plus « vertes ». Cela démontre que les individus n'ont pas de calendriers fixes, mais montrent un comportement plastique en réponse aux conditions environnementales. Le chapitre complète les connaissances de base sur les exigences écologiques de l'espèce en hiver.

L'importance des derniers sites d'hivernage a été explorée plus en détail au **chapitre 3**. Nous montrons ici comment les Busards cendrés font face au paradoxe de Moreau: comment tous les migrateurs paléarctiques pourraient (i) se maintenir au Sahel et (ii) se préparer à la migration de printemps alors que les conditions environnementales se détériorent continuellement pendant leur séjour ? Hivernant exclusivement dans la zone sahélienne, les Busards se retrouvent à la limite sud de la zone sahélienne sur le dernier site d'hivernage et n'ont pas d'autre choix que de faire face à la dégradation des conditions environnementales au fur et à mesure que leur habitat se dessèche en hiver. L'abondance des proies (nombre de sauterelles associées à la verdure de la végétation) sur les sites d'hivernage des Busards cendrés diminue en effet au cours de la période hivernale sèche. Les Busards ont réagi à cette diminution de la disponibilité alimentaire en augmentant régulièrement leur temps de vol au cours de la deuxième moitié de l'hiver. Les individus dans les zones où les valeurs de l'indice de végétation (NDVI) diminuent davantage augmentent davantage leur temps de vol, ce qui suggère que la plus faible abondance de proies nécessite une recherche plus intensive de nourriture pour répondre aux besoins en énergie. Lorsque le dernier site d'hivernage présentait des valeurs de NDVI plus faibles et une abondance de nourriture probablement moindre, les busards initiaient leur migration plus tardivement au printemps, avec pour conséquence une arrivée plus tardive sur leur site de reproduction. Ces résultats indiquent que la fin de la période d'hivernage pourrait constituer un goulot d'étranglement au cours du cycle annuel, avec des effets possibles sur la saison de reproduction.

Le **chapitre 4** décrit le cas d’un mâle adulte de Busard cendré suivi par GPS et ayant estivé (pendant la saison de reproduction donc) en Afrique. En établissant un lien entre la connaissance détaillée des mouvements de l'oiseau et les données environnementales obtenues par télédétection (NDVI), nous montrons que l’estive africaine dans ce cas était probablement liée à une saison de reproduction exceptionnellement difficile l'année précédente plutôt qu'à un effet des conditions météorologiques défavorables rencontrées en hiver, ou une tentative de migration infructueuse. Ce chapitre fournit donc un exemple des effets de report (‘carry-over effects’) de la saison de reproduction aux saisons suivantes.

Après ces études détaillées sur l’écologie hivernale, le **chapitre 5** donne un aperçu circannuel des distances de vol quotidiennes et totales des busards cendrés. Le suivi GPS de 29 busards cendrés dans se reproduisant en France, aux Pays-Bas et au Danemark a montré qu’ils volaient entre 35 653 et 88 049 km / an, dont 28,5% en moyenne en période de migration. Les distances journalières moyennes au cours de la migration étaient de 296 km j^{-1} en automne et de 252 km j^{-1} au printemps. Étonnamment, les distances journalières des mâles pendant la reproduction (217 km j^{-1}) étaient proches de celles de la migration, alors que les femelles nicheuses se déplaçaient beaucoup moins (101 km j^{-1}) que les mâles. En termes de distance de vol journalière, la saison de reproduction semblait presque aussi exigeante que les périodes de migration pour les mâles. Au cours des six mois d’hiver, les deux sexes se sont moins déplacés (respectivement 114 et 128 km j^{-1} pour les femelles et les mâles) que pendant la migration. Les Busards ont donc parcouru des distances journalières plus courtes en hiver. La période hivernale semble donc être la période la moins exigeante (du point de vue énergétique) du cycle annuel et pourrait servir de tampon pour contrer les effets de report de la saison de reproduction ou la migration automnale. Cependant, l'exemple du Busard cendré mâle ayant estivé en Afrique et décrit au chapitre 4, ainsi que les effets de report possibles décrits au chapitre 3, suggèrent qu'il pourrait s'agir d'une conclusion prématurée.

S’intéressant maintenant à la période de reproduction, le **chapitre 6** décrit la variation de l’activité et de la taille du domaine vital des Busards cendrés mâles dans la principale zone de reproduction des Pays-Bas. Bien qu’ils nichent dans les mêmes zones, la taille des domaines vitaux variait d’un facteur cinq, reflétant les différentes stratégies d'utilisation de l'espace. Les individus dont le domaine vital était plutôt petit se sont relativement peu déplacés et ont exploité quelques parcelles d’alimentation de haute qualité qu’ils ont visitées fréquemment. Les individus ayant des domaines vitaux relativement vastes ont parcouru de plus longues distances, ont rarement revisité les mêmes groupes de parcelles mais ont plutôt exploré de nouveaux sites d’alimentation. Les mâles avaient un domaine vital plus petit les années où les proies étaient abondantes comparativement aux années où la ressource était limitée. Ce chapitre indique qu'un habitat d'alimentation de haute qualité est nécessaire pour limiter les distances parcourues par les Busards. A défaut, leur charge de travail quotidienne serait d’un même ordre de grandeur que lors des journées de migration, comme indiqué dans le chapitre 5.

Pour améliorer l'habitat d'alimentation dans les zones de reproduction néerlandaises, une nouvelle mesure agroenvironnementale (MAE) pour les Busards cendrés a été décrite et testée au **chapitre 7**. Les MAEs actuelles, telles que les bandes herbées le long de champs, qui ont pour objectif d'améliorer les conditions de recherche de nourriture (densités de campagnols) pour les Busards sont inefficaces, car les proies sont difficiles à capturer dans les herbes hautes des jachères. La mesure ‘Birdfields’ (« des champs pour les oiseaux ») combine des bandes de jachères pour augmenter le nombre de campagnols et des bandes de luzerne, les campagnols étant accessibles après la récolte de cette dernière. Nous avons constaté que le nombre de campagnols était généralement plus élevé dans les jachères. Les busards cendrés suivis par GPS utilisaient intensément les Birdfields après la tonte, préférant les bandes tondues aux bandes non tondues. Ainsi, la disponibilité des proies semblait plus importante que leur abondance. Par conséquent, Birdfields, en tant que MAE ciblée pour les Busards cendrés, est plus efficace que les MAEs précédentes en raison de l’accessibilité accrue des proies. Birdfields présente un autre avantage: il est considérablement moins cher en raison de la récolte de la luzerne. La nouvelle MAE décrit dans ce chapitre offre la possibilité d’améliorer l’habitat de nidification pour les busards cendrés et d’autres espèces prédatrices de campagnols dans les paysages agricoles intensifs.

Cette thèse a élargi nos connaissances sur les exigences écologiques des Busards cendrés pendant l’hiver et pendant la saison de reproduction, connaissances qui peuvent être utilisées pour améliorer les mesures de conservation de l’espèce. Le **chapitre 8** résume les conclusions des chapitres précédents tout en soulevant des questions pour les recherches futures. En outre, une mise à jour des taux de mortalité au cours des quatre cycles annuels suggère une augmentation de la mortalité en hiver, et lors de la migration de printemps, ces dernières années. La conséquence principale du paradoxe de Moreau pourrait donc être une mortalité accrue pendant la migration printanière, plutôt qu’un effort accru de recherche de nourriture ou même une mortalité supérieure à la fin de l’hiver. Ces évolutions indiquent que, bien que nous pensions que la principale limitation pour les populations de Busards cendrés se situe dans les zones de reproduction, l’hiver pourrait devenir, ou est déjà devenu, la saison limitante.

Zusammenfassung

Populationsregulierung bei Langstreckenziehern ist kompliziert, da diese im Jahresverlauf mehrere, weit auseinander liegende Gebiete benutzen, deren Aufnahmefähigkeit sehr unterschiedlich sein kann. Um die Populationsdynamik und den Einfluss von Umweltveränderungen auf Populationen zu verstehen, sind Erkenntnisse über Bruterfolg, Sterblichkeit, Verbreitung und Habitatnutzung wie auch deren zeitliche und räumliche Variation nötig. Dies ist sehr wichtig, da langstreckenziehende Arten abnehmen, vor allem Arten der Agrarlandschaft. Die Intensivierung der Landwirtschaft hat in Europa nachweislich zu einer dramatischen Abnahme von Vögeln der Agrarlandschaft geführt. Arten, die auch in ihrem Überwinterungsgebiet abhängig sind von Agrarlandschaften, sind doppelt gestraft („double jeopardy"), da schnelle und drastische Veränderungen der Landschaftsnutzung die Habitate ihrer Überwinterungsgebiete verschlechtern und zerstören. Um solche Arten zu schützen, brauchen wir detaillierte Kenntnisse ihrer ökologischen Bedürfnisse in den verschiedenen Phasen ihres Jahreszyklus.

Leider ist der Wissensstand über den Jahreszyklus vieler Langstreckenzieher noch lückenhaft. Lange lag der Fokus vieler Studien auf Untersuchungen im Brutgebiet und erst seit Kurzem, dank immer kleiner werdender GPS-Sender, bekommen wir mehr Einblicke in die anderen Phasen des Jahreszylus, nämlich Zug und Überwinterung. Dennoch, nicht alles kann am Bildschirm beurteilt werden und Feldarbeit in den Überwinterungsgebieten bleibt nötig, um zu begreifen was in Wirklichkeit dort geschieht. Allerdings ist Feldarbeit in Afrika eine Herausforderung infolge schwieriger Logistik und unsicheren politischen Situationen. Gleichwohl bleibt eine Kombination von Daten moderner technische Errungenschaften, wie GPS-Sendern, mit Feldarbeit und Fernerkundungsdaten eine wertvolle Vorgehensweise, um mehr über die verschiedenen Phasen des Jahreszyklus von Langstreckenziehern zu lernen.

In dieser Doktorarbeit habe ich hochmoderne GPS-Sender in Kombination mit traditioneller Feldarbeit und Fernerkundungsdaten verwendet, um unser Wissen über die Wiesenweihe *Circus pygargus* zu erweitern. Die Wiesenweihe ist ein solcher Langstreckenzieher, der großen Veränderungen seines Lebensraumes in der Agrarlandschaft in den Brutgebieten sowie den Überwinterungsgebieten ausgesetzt ist. Die Feldarbeit in den Brutgebieten wurde vor allem in den Niederlanden durchgeführt, aber unser Datensatz konnte, dank Zusammenarbeit mit unseren dänischen und französischen Kollegen, erweitert werden. Während des Winters wurden Felddaten im Senegal gesammelt, wo viele der nord-westeuropäischen Brutvögel überwintern. Da Wiesenweihen ungefähr die Hälfte des Jahres in den afrikanischen Überwinterungsgebieten verbringen und die Bedingungen dort ihre Populationen beeinflussen können, durch Überlebensraten und sogenannte Übertragungseffekte (in Engl. *carry-over effects*), startet diese Doktorarbeit aus einer afrikanischen Perspektive.

Im **2. Kapitel** geben wir anhand eines großen Datensatzes von mit Sendern verfolgten Wiesenweihen eine detaillierte Beschreibung der Nutzung von Überwinterungsgebieten im

Lauf des Winters im Bezug auf jährlich wechselnde Umweltbedingungen. Die Vögel hatten durchschnittlich drei Überwinterungsgebiete, die sie in einem Winter hintereinander aufsuchten und zu denen sie zwischen verschiedenen Jahren starke Ortstreue zeigten. In den Ankunftsgebieten (erstes Gebiet, das genutzt wird nach Überquerung der Sahara), verblieben die Wiesenweihen ca. einen Monat. Diese Gebiete, die in der nördlichen Sahelzone liegen, werden hauptsächlich durch natürliche und spärliche Vegetation gekennzeichnet. Zwischengebiete und Abzugsgebiete (letztes Gebiet vor Abzug) liegen grundsätzlich weiter südlich in der Sahelzone und werden durch landwirtschaftliche Nutzung und natürliche Habitate gekennzeichnet. Wiesenweihen bevorzugten Gebiete mit einer höheren Diversität an Habitaten verglichen mit Zufallsgebieten. Aktionsräume waren größer und Flugaktivität höher in Abzugsgebieten und höher bei Individuen, die in trockeneren Gebieten verblieben. Wir konnten zeigen, dass bei Individuen, die über mehrere Jahre verfolgt werden konnten, die Größe des Aktionsraums nicht abhängig war von wie viel grüne Vegetation (Grün-Index - Normalized Difference Vegetation Index) vorhanden war. Allerdings flogen die Vögel mehr Kilometer im selben Gebiet in trockeneren Jahren verglichen mit grüneren Jahren. Der Zeitpunkt intratropischer Bewegungen (von einem Gebiet zum nächsten) wurde auch angepasst an die jährlich verschiedenen lokalen Umweltbedingungen, die die Vögel erfuhren. Individuen blieben kürzer in einem Ankunftsgebiet und wechselten früher in das nächste Gebiet in trockeneren Jahren und kamen früher im Abzugsgebiet an in grüneren Jahren. Dies zeigt, dass Individuen keinen festen Zeitplan haben, sondern plastisches Verhalten als Antwort auf Umweltbedingungen zeigen. Dieses Kapitel liefert damit einen Beitrag zum allgemeinen Wissen über die ökologischen Bedürfnisse der Art im Winter.

Die Bedeutung der Abzugsgebiete (letztes Überwinterungsgebiet) wurde weiter untersucht im **3. Kapitel**. Hier zeigen wir wie Wiesenweihen mit Moreau’s Paradox umgehen: wie können sich all die paläarktischen Zugvögel in der Sahelzone erhalten und sich dort für den Frühjahrszug vorbereiten in sich kontinuierlich verschlechternden Bedingungen? Wiesenweihen, die ausschließlich in der Sahelzone überwintern, befinden sich am südlichen Rand der Sahelzone in ihren Abzugsgebieten und haben dort keine andere Wahl als sich den dort herrschenden und sich während ihres Aufenthalts durch zunehmendes Austrocknen verschlechternden Bedingungen zu stellen. Die Nahrungsverfügbarkeit (Heuschrecken Anzahlen waren vom Grün-Index abhängig) in den Überwinterungsgebieten der Wiesenweihen nahm tatsächlich ab im Laufe des Winters. Die Vögel reagierten auf die geringere Nahrungsverfügbarkeit durch ständige Zunahme ihrer täglichen Flugaktivität in der zweiten Winterhälfte. Individuen in Gebieten mit stärkerer Abnahme von Grün-Index Werten erhöhten ihre Flugaktivität mehr, ein Zeichen, dass geringere Nahrungsverfügbarkeit mehr Nahrungssuche erfordert um die Energiebedürfnisse zu decken. Die offensichtliche Konsequenz davon war, dass Wiesenweihen später abzogen im Frühjahr und folglich später im Brutgebiet ankamen, wenn ihr Abzugsgebiet niedrigere Grün-Index Werte hatte und damit wahrscheinlich eine geringere Nahrungsverfügbarkeit aufwies. Diese Ergebnisse weisen darauf hin, dass das Ende der Überwinterungsperiode ein Engpass (in Engl. *bottleneck*) im Jahreszyklus sein könnte, mit möglichen Übertragungseffekten zur Brutsaison hin.

Das **4. Kapitel** beschreibt den Fall eines adulten GPS-besenderten Wiesenweihen Männchens, das in Afrika übersommerte. Durch detaillierte Bewegungsdaten des Vogels mit Fernerkundungsdaten (Grün-Index) zu verbinden, konnten wir zeigen, dass die Übersommerung in diesem Fall wahrscheinlich auf eine außergewöhnlich anstrengende Brutsaison zurückzuführen war und nicht auf ungünstige Wetterbedingungen während des Winters oder einen misslungenen Versuch abzuziehen. Dieses Kapitel gibt somit ein Beispiel für Übertragungseffekte aus der Brutzeit in nachfolgende Phasen des Jahreszyklus.

Nach diesen detaillierten Studien zur Überwinteringsökologie, gibt das **5. Kapitel** einen weiteren Ausblick auf den ganzen Jahreslauf und beschreibt tägliche und Gesamtflugstrecken von Wiesenweihen. Daten von 29 Wiesenweihenmännchen, die in ihren Brutgebieten in Frankreich, den Niederlanden und Dänemark mit GPS-Sendern ausgerüstet wurden, zeigten, dass die Weihen jährlich zwischen 35 653 und 88 049 km fliegen, wovon nur ca. 28,5 % auf dem Zug zurückgelegt wird. Durchschnittlicher täglicher Abstand auf dem Zug waren 296 km pro Tag im Herbst und 252 km pro Tag im Frühjahr. Überraschenderweise legten Männchen während der Brutzeit beinahe so viele Kilometer zurück wie auf dem Zug (217 km pro Tag), während Weibchen bedeutend weniger flogen als Männchen (101 km pro Tag). Bezüglich der täglich zurückgelegten Strecke schien die Brutsaison beinahe genauso anspruchsvoll für Männchen zu sein wie die Zugzeit. Während der sechs Wintermonate hingegen flogen beide Geschlechter weniger als auf dem Zug (114 und 128 km pro Tag für Weibchen und Männchen). Sie legten also kürzere tägliche Flugstrecken zurück während des Winters. Der Winter scheint deshalb die Phase des Jahreszyklus zu sein, die am wenigsten (energetisch) anspruchsvoll ist und die als ein Puffer wirken könnte, um Übertragungseffekte aus der Brutzeit oder dem Herbstzug abzufangen. Allerdings zeigt das Beispiel eines übersommernden adulten Männchens im 4. Kapitel, dass dies eine vorzeitige Schlußfolgerung sein könnte.

Das **6. Kapitel** bringt uns zum Brutzeit Teil des Jahreszyklus und beschreibt die Variation in Aktivität und Aktionsraumgröße von Wiesenweihenmännchen im niederländischen Brutgebiet. Obwohl Individuen im selben Gebiet brüteten, variierten ihre Aktionsräume fünffach, was verschiedene Raumnutzungsstrategien widerspiegelt. Individuen mit relativ kleinem Aktionsraum flogen relativ wenig und nutzten einige wenige hochqualitative Nahrungsflächen, welche sie oft wieder besuchten. Individuen mit relativ großem Aktionsraum flogen größere Abstände und nutzen selten dieselben Nahrungsflächen sondern erkundeten stattdessen neue Gebiete. Männchen hatten kleinere Aktionsräume in Jahren mit höherer Nahrungsverfügbarkeit als in Jahren mit wenig Beute. Dieses Kapitel weist darauf hin, dass hochqualitative Nahrungsflächen nötig sind, um zu verhindern, dass Weihen lange Abstände fliegen müssen, was sonst ihren täglichen Arbeitsaufwand erhöht selbst bis zu einem Ausmaß ähnlich Zugtagen (siehe 5. Kapitel).

Um Nahrungsflächen für die Wiesenweihen zu verbessern wurde im **7. Kapitel** eine neue Agrarumweltmaße (AUM) beschrieben und getestet. Heutige AUM, wie zum Beispiel Ackerrandstreifen, die die Beutedichte (z.B. Feldmaus) erhöhen sollen, sind für Weihen ineffizient, da die Beute schwierig erreichbar ist in der hohen Brachvegetation. Vogelfelder („Birdfields“) kombinieren Streifen von Brachvegetation, in denen hohe Beutedichten vorkommen, mit Streifen von Luzerne, auf denen durch Mahd die Erreichbarkeit der Beute erhöht wird. Wir stellten fest, dass die Mausedichte in der Brachvegetation generell höher war. Wiesenweihen, die mit GPS-Sendern ausgerüstet waren, nutzten die Vogelfelder intensiv nach der Mahd und bevorzugten gemähte vor ungemähten Streifen. Somit scheint die Beuteverfügbarkeit wichtiger zu sein als die Beutedichte. Folglich sind Vogelfelder, als gezielte AUM für Wiesenweihen, effektiver als bisherige AUM durch die erhöhte Beuteverfügbarkeit. Ein weiterer Vorteil der Vogelfelder ist, dass sie bedeutend günstiger sind als andere AUM durch die Erträge der Luzerneernte. Die in diesem Kapitel beschriebene neue AUM zeigt Möglichkeiten zur Verbesserung von Nahrungsflächen für Wiesenweihen und anderen mausefressenden Arten in der intensiven Agrarlandschaft auf.

Diese Doktorarbeit hat unser Wissen über die ökologischen Bedürfnisse der Wiesenweihen während des Winters und der Brutzeit erweitert, was genutzt werden kann, um Schutzmaßnahmen für die Art zu verbessern. Das **8. Kapitel** fasst die Ergebnisse der vorigen Kapitel zusammen und wirft Fragen für zukünftige Untersuchungen auf. Zusätzlich weist eine aktualisierte Analyse der Sterblichkeitsraten während der vier Phasen des Jahreszyklus darauf hin, dass die Sterblichkeit im Winter und während des Frühjahrszuges in den letzten Jahren zugenommen hat. Dies könnte bedeuten, dass die Hauptfolge von Moreau’s Paradox eine erhöhte Sterblichkeit im Frühjahr ist und nicht der zunehmende Aufwand zur Nahrungssuche am Ende des Winters oder Sterblichkeit im Winter selbst. Diese Entwicklungen weisen darauf hin, dass die Beschränkungen der Wiesenweihenpopulationen, obwohl wir dachten, dass diese in den Brutgebieten liegen, im Winter liegen könnten oder gar bereits liegen.


NAVARA

Acknowledgements

Well, here I am, sitting and thinking on how to write in a much too short time something about a (maybe much too) long period. The reason that only very little time is left is however a good one: I just enjoyed three months of intensive fieldwork in one of the most productive years for our Montagu's Harriers in East Groningen. Good choice!

My Montagu's Harrier story started in 2009 when Klaus-Michael Exo, the supervisor of my bachelor thesis on Common Redshank at the University of Oldenburg, sent me to his collaborators in Groningen to see some harriers. I just stayed a long weekend in the summer house with Jitty, but the experience was great and I directly fell in love with the beautiful Monties. After that I gladly accepted the possibility offered by Chris Trierweiler and Ben Koks to write my Master's thesis about stopover site ecology of Montagu's Harriers in East Morocco and join into some great adventures.

A big thanks to all participants of three great Morocco expeditions in 2010 and 2011. Chris and Ben who drove me down all the way from Holland to Morocco, sleeping in the back of the car, not understanding a single Dutch sentence. Rob Buiter who joined us during the first trip and witnessed our first encounter with satellite-tagged male Montagu's Harrier *Franz* on the roost on the high plateaus near Ain Bni Mathar (everyone heard us yelling on Vroege Vogels, but you saw how high we jumped!). Hans Hut who drove down with Ben for the second expedition and Harold van der Meer and Sjoerd Sipma taking part in the third (Almut and the three Dutch guys of 47 years old; notes might still be found in the large book at the police control post where we had to write down our passport numbers, names of parents etc. each time we passed through Tendrara). Seeing Montagu's Harriers in one of their most important stopover regions and observing them in such a different environment is special, especially when you encounter the same individual some two or three weeks later in the vast fields of the Oldambt displaying high in the air to attract a female. Chris, you were a great mentor and are a good friend; I always modelled myself on you and we share more than only harriers but also horses and donkeys. Thanks for supervising me and teaching me how to tag harriers!

During the summer of 2010, I shared the summer house with Adri Clements (thanks for teaching me my first Dutch) and enjoyed my first harrier breeding season in the flat and sometimes desert like agricultural fields of East Groningen. If it wasn't for the harriers, I might have preferred the Black Forest or even Iceland. But they made me stay. After the second Morocco expedition and being in the middle of writing up my Master's thesis, Ben offered me a position as staff member at the Dutch Montagu's Harrier Foundation (toen Werkgroep Grauwe Kiekendief, inmiddels Grauwe Kiekendief - Kenniscentrum Akkervogels) which I gladly accepted. In 2011, the first weeks of my contract started with a great experience: my first expedition to West Africa. Thanks to Leen Smits we were able to travel to Niger in pursuit of our satellite-tagged harriers. And since the birds don't care about borders, we managed to get more visas stamped in our passports in Niamey and drove all the way through Burkina Faso into Mali and back. It was a memorable trip thanks to the good company of Abdoulaye Harouna and Kailou Moussa, Ben and Leen. It is a pity that such a voyage is nowadays much too risky (only bold and a little crazy people still dare to do such things and I envy you for that Rob, Jan and Leo). But my first trip to Senegal with French colleagues in 2013 showed me that I could easily conduct my fieldwork there, being able to drive just where you want (nearly always) and not needing armed guards. Thanks to Steve Augiron who introduced me to Albert Dely Faye in Diabel, Senegal. Albert helped us during all our expeditions in Senegal with logistics, grasshopper counts and finding harrier roosts. I am very happy to have such a friend. Albert, je te remercie pour tout ce que tu as fait pour nous ! It was a really great pleasure to travel and work with JF (Jean-François) Blanc and his brother Vincent Blanc. Thanks for all your help and discussions about the world and more, I enjoyed our trip to Kedougou a lot, merci! Ben, Wim Mullie, Joris van Alphen and Christiaan Both were also taking part in one or several of the Senegal expeditions, thank you all. Thanks to Franck Noël for the pellet analysis.

I am very grateful to Wim Mullié, Hanneke Dallmeijer and Jan Veen who offered me the great opportunity to join into an expedition and help tagging the first Royal Terns, Caspian Terns and Slender-billed Gulls on Ile-aux-Oiseaux in the Sine Saloum Delta in Senegal. Staying on the island with you in a stationary camp was a new experience of fieldwork in Africa for me and I enjoyed it a lot. Thanks to Adama Lene and the whole team for this memorable stay. I enjoyed even more that we collaborated for the analyses of the data from the tracked birds afterwards and still do. It is a real pleasure to work with you and I am looking forward to more exchanges, analyses and manuscripts!

These expeditions to Senegal were already part of my PhD project. Since I already worked for the foundation in 2011 and 2012, there was no big change when I started the PhD. I just continued what I was doing and had a lot of freedom to choose what to do (which was not always an advantage since making choices is not the easiest thing to do and certainly not my strength). Luckily, we were able to apply for a position at the University of Groningen together with Christiaan and managed to start the PhD project as one of the Sandwich positions funded for two years by the Ubbo Emmius grant. The disadvantages of this construction became soon obvious. Being officially obliged to spend the second part of the PhD at another institution in another country, I had to move to France. Already being not really part of the group due to my external bonds with the Dutch Montagu's Harrier Foundation and not being in the office regularly, it also didn't help to be away for such a long time. Unfortunately, I might cite Bilbo Baggins at this point (only meaning it well!): "I don't know half of you half as well as I should like". I still enjoyed very much being part of the Conservation Ecology Group and am very thankful to everyone there: Christiaan, Eldar, Elena, Hacen, Irene, Janne, Jelle, Jelmer & Nicole, Jeroen O., Jeroen R., Jesse, Jos, Joost, Julia, Koosje, Lucie, Ruth, Maaike, Marco, Marion, Martijn, Maurine, Mo, Pieter, Raymond, Richard, Rienk, Sajad, Theunis, Xuelai, Yvonne and everyone else from the nice coffee breaks. A big thanks to Joyce and Ingeborg who always helped me finding answers to all my questions at the university and to Corine and Paul for help with administrative obstacles.

After moving to France, I counted myself lucky to be a sandwich PhD. I just loved it there. The landscape, the people, the villages, the food, the Pineau des Charentes, the donkeys. I am very

grateful that I had this great opportunity to live in France. Thanks to everyone who made this such a pleasant period in my life: Adeline and her family with all the people at the Écurie les Giraudières, Helena and Andy with Jojo and Rozie, Vincent et Sonia avec Noë, Armel et Simon, Stephanie et Michel, Sophie and family, Karin et Francois, David and Jane, Jean-Claude, Jean-Claude Nicollas et famille, Mr et Mm Reberry, Elsa et famille, Marion, Pierre et Stefanie, Sylviane et Jacky, Benoit et Christelle, team Asinerie, Pamela, Guillaume. Thanks to all the colleagues and friends from the lab at Chizé: Anaïs, Alex, Alexis, Alicia, Bertrand, Camille, Carine, Fabrice, Gaël, Gaëtane, Jessica, Jodie, Karine, Laura, Licia, Louis, Marie, Marilyn, Martine, Nico, Paul, Romain, Rui, Sam, Thierry, Thomas, and all the other people from the lab and Paizay-le-Tort!

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When I realized that I would not manage to finish the whole project on my own and was at the brink of giving up, I had great help from Mireille Lusseau, Nicolien Wieringa and Lidy Oosterhof. Thank you all very much for bringing me back on track! I am deeply grateful to Janne and all the Bonobo's who rescued and accommodated men when I came back to the Netherlands, thank you so much for your warm welcome, it meant so much to me! And thanks to you Lenze, I had the great pleasure to live in the Carex farm in Harkstede…

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Le Grand Manège
Saumur
Canon

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