Migrants in double jeopardy

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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-distance 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 been 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
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 ($\mu$) 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 Harriers 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

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.