Szent István University
Postgraduate School of Veterinary Science

# Large scale breeding site selection and non-breeding individual movement patterns of Red-footed Falcons

PhD thesis

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In god we trust, all others bring data.[1]

*Adult female Red-footed Falcon on a rainy day. Photo by Peter Fehérvári*

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[1] Hastie T., Tibshirani R., Friedman J., Hastie T., Friedman J., Tibshirani R., **The elements of statistical learning**, volume 2, Springer, 2009.

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# Summary

Understanding the proximal and ultimate causes of avian distribution patterns has been in the center of ecology and biogeography research. In this thesis I present a multidisciplinary approach on how to link environmental factors with a species' breeding site choice, and individual movement patterns, and show that understanding this relationship may yield direct conservation benefits.

The focal species of the thesis is the Red-footed Falcon (*Falco vespertinus*), an enigmatic colonial raptor of high international conservation concern. One of the identified threatening factors responsible for the worldwide population decline is the shortage of suitable colonial nesting sites. Due to a severe population decline and shrinkage of distribution range in the past decades, the Red-footed Falcon has gained top priority in both worldwide and Hungarian nature conservation. As a facultative colonial breeder, in Hungary, this species predominantly nests in rookeries. The number of Rooks (*Corvus frugilegus*) has also dramatically fallen recently, but population decline did not affect the large scale breeding distribution of this species.

In my first case study I show how landscape scale habitat variables affect the presence probability of Red-footed Falcons at a given potential colony in the current and historical breeding ranges. We used a potential colony home-range size, estimated from observed home-range sizes in order to determine the scale of influential habitat variables. According to our results, a potential cause of the observed range shift is the urbanization of Rooks in certain regions of Hungary. The ratio of forests and open water surfaces within the potential home-range had negative, while the ratio of grasslands had a positive effect on the probability of Red-footed Falcon presence. None of our models predicted Red-footed Falcon presence at colonies outside the current breeding range, suggesting that a probable increase in Red-footed Falcon population numbers will not be accompanied by the expansion of the current breeding range. In theory, the lack of potential nesting sites can easily be resolved by establishing artificial nest-box colonies. However, the key to a successful large scale nest-box scheme is to provide these artificial colonies in habitats suitable for the species, as I show it in the second case study. A Hungarian-Serbian project aimed to establish such nesting facilities in northern Serbia; though, the lack of recent full scale habitat surveys hindered the designation of the locations of these artificial nesting sites. I used five different species distribution models to model the distribution of nest-sites on a

10x10 km grid in Hungary and in Romania. I then used the ensemble predictions of the best performing models to project the probability of Red-footed Falcon nest-site presence in Northern Serbia. The predictions classified all the currently known colonies in the predicted area correctly. Our results suggest that the potential breeding distribution in Serbia is similar to that of two decades ago, thus large scale land use changes are unlikely to be responsible for the reported population decline. We have also identified conservation target areas that constitute 11.5% of the extent of the modeled area. These identified target areas may serve as a basis for future conservation measures like allocating monitoring efforts, establishing artificial colonies for Red-footed Falcons and designating future Natura 2000 sites in Serbia.

Red-footed Falcons are gregarious trans-equatorial migrants, forming up to several thousand strong evening roost sites after the breeding season and before commencing migration. This pre-migration period is presumed to play a major role in defining the survival of long-range migrants. Here I investigate the autumn movements of 8 individuals caught and satellite-tagged within the Carpathian Basin. I found that birds may use multiple roost sites that can be separated by large distances. A single individual's home range was 88 km$^2$ and was near concentric to the roost site. Two individuals traveled to southern Ukraine soon after tag-deployment. The night localization points of birds marked out 2 and 5 yet unknown potential roost sites in Hungary and in the Ukraine, respectively. Using the data of an international weekly survey (2006–2011) carried out in the Carpathian Basin, I cross-referenced the departure dates of tagged individuals with the 6 year means of counted individuals. The tagged birds commenced migration with the first 25% percent of the surveyed population. My results demonstrate that even a small number of satellite tagged birds show behavioural plasticity in terms of roost site selection indicating that post-breeding foraging habitat choice decisions may have substantial variability.

Tropical rainforests act as ecological barriers to avian migrants, yet the reasons for this are unclear. I report evidence that dense and stochastic precipitation substantially explains the trajectories of falcons migrating within the African rainforest. I used 11 years of National Oceanic and Atmospheric Administration's highest resolution daily rainfall estimates to calculate the risk of migrants encountering dense rain. My analyses revealed the long-term existence of a north-south corridor in which the risk of precipitation was considerably lower than in surrounding areas. The migration routes of satellite-tracked Red-footed Falcons converged into this corridor, in which individuals avoided immediate concentrations of rain. My examination of published studies indicated that a second falcon species used the same corridor, while individuals of a third species migrated 1500 kilometres west through another lower risk corridor we had identified. These findings suggest the importance of rainfall in shaping the migration patterns of birds that pass through rainforests.

# Chapter 1

# Introduction

Birds are amongst the most widespread and mobile vertebrates of the world (Reilly, 2008). Certain species like the house sparrow (*Passer domesticus*) or the common kestrel (*Falco tinunculus*) inhabit several continents (Del Hoyo et al., 1992), while others like the Chaplin's Barbet (*Lybius chaplini*) have very specialized and localized or even patchy distributions (Sibley and Monroe, 1990). From open oceans, the Arctics or high mountain ranges they populate the most inhospitable parts of our planet.

Understanding the proximal and ultimate causes of avian distribution patterns has been in the center of ecological and biogeographical research (Jones, 2001; Karanth et al., 2013; Kissling et al., 2012; Pearman et al., 2014; Root, 1988). Birds are excellent model systems to study large scale distribution patterns as most species are highly mobile and their ability to travel large distances allows for less constrained spreading capabilities compared to any other taxa (Berthold, 1996). Before I move on it is important to define the term distribution from an avian perspective. Individuals of a species utilize resources usually in well definable areas, so-called home-ranges, and these resources are often exploited for a discrete life history event, such as reproduction (Calenge and Dufour, 2006; Matthiopoulos, 2003). In case of sedentary birds (spending their full life cycle within or near their breeding area) my definition of distribution is the minimum area around all known individual home-ranges of a species. However, roughly half of the approx. 9000 bird species are migratory to some extent (Alestram, 1990; Newton, 2010a). Defining the distribution of these species is challenging, and probably the most yielding approach is to characterize distribution based on the presence of individual home-ranges in respect to which life history event they utilize it for. Thus, we can define breeding, and non-breeding distributions. In the latter case we may differentiate pre-migratory, passage, stop-over, and wintering distributions, which can often be separated by enormous distances.

In general, most avian distribution studies concentrate on breeding distribution (Fehérvári et al., 2012; Huntley et al., 2007; Mac Arthur, 1959; Pagen et al., 2000), mainly due to methodological constraints. One of the most important constrain is detecting the presence of individuals in a given area. Most birds become central place foragers (Rosenberg and McKelvey, 1999), often display (Burnside et al., 2014) or vocalize (Chappell et al., 1995) in their breeding period, thus assessing a species in a given habitat is less challenging. Within a given breeding distribution and within individual home-ranges, birds utilize resources, such as breeding sites (Fehérvári et al., 2009)or foraging areas (Palatitz et al., 2011). The shape and extent of a given breeding home-range has considerable species-specific variability (Brown et al., 1996; Holbrook, 2011; Mitani and Rodman, 1979; Odum and Kuenzler, 1955; Pigot et al., 2010). This variability, amongst others, can be considered as a function of species-specific traits, and within species individual quality. Habitat selection and breeding site selection (i.e. the location of the nest) are intimately linked, however emphasis in home-range selection may vary amongst species or between populations. For instance, members of the Falco genus of the Falconiformes order do not build nests, instead they occupy either nests of other species or use natural cavities and cliffs (Newton, 2010b). In their case breeding site selection needs to be emphasized in relation to habitat selection (Bustamante, 1997; Catry et al., 2009; Harrison et al., 2003; Jones, 2001; Lopez-Lopez et al., 2007).

Avian migrants have astonished laymen and scientists alike for centuries with their athletic achievements when it comes to traveling. Some of the most fascinating migratory routes discovered recently entail traversing thousands of kilometers in one flight or crossing inhospitable areas like deserts or oceans (Alerstam, 2011; Battley et al., 2011; Bridge et al., 2011; Klaassen et al., 2011; Smith et al., 2014; Strandberg et al., 2009; Suryan et al., 2006). Both of these remarkable capabilities are demonstrated by the Amur Falcon (*Falco amurensis*), that has the longest migratory routes of all raptors in the world (Symes and Woodborne, 2010). These birds breed in Mongolia, Amurland and northeast China, and winter in southern Africa. They semiannually cross the Arabian Sea to and forth their wintering sites with a single non-stop flight. The fascinating part of their journey is that there seems to be evidence that this single non-stop flight is in fact initiated from the Bengal Bay (i.e. the north eastern coasts of India) instead from the south western coast that one would intuitively expect (Fig. 1.1, see `www.satellitetracking.eu` for details).

The boom in technology enabling individual tracking of avian migrants now allows us to reveal such journeys, and has reformed research in migration ecology (Bridge et al., 2011; Guilford et al., 2011). The range of available devices to deploy on birds is overwhelming, from Platform Transmitting Terminals (PTTs), GPS tags, GPS-GSM tags, light-level geolocators to GPS loggers, even species with as small as 10–12 gram average body weights can be individually tracked. However, a common trade-off of tracking, regardless of technology used, is that sample size is limited by the relative high costs of devices. Despite this, the individual migratory trajectories drawn by the tracked individuals help us better understand how birds cope with the challenges en-route and during the non-breeding period. Without tracking, it would be virtually impossible to identify migration strategy types (Klaassen et al., 2011), critical stopover sites (Guo-Gang et al., 2011) or potential high risk areas (Milner-

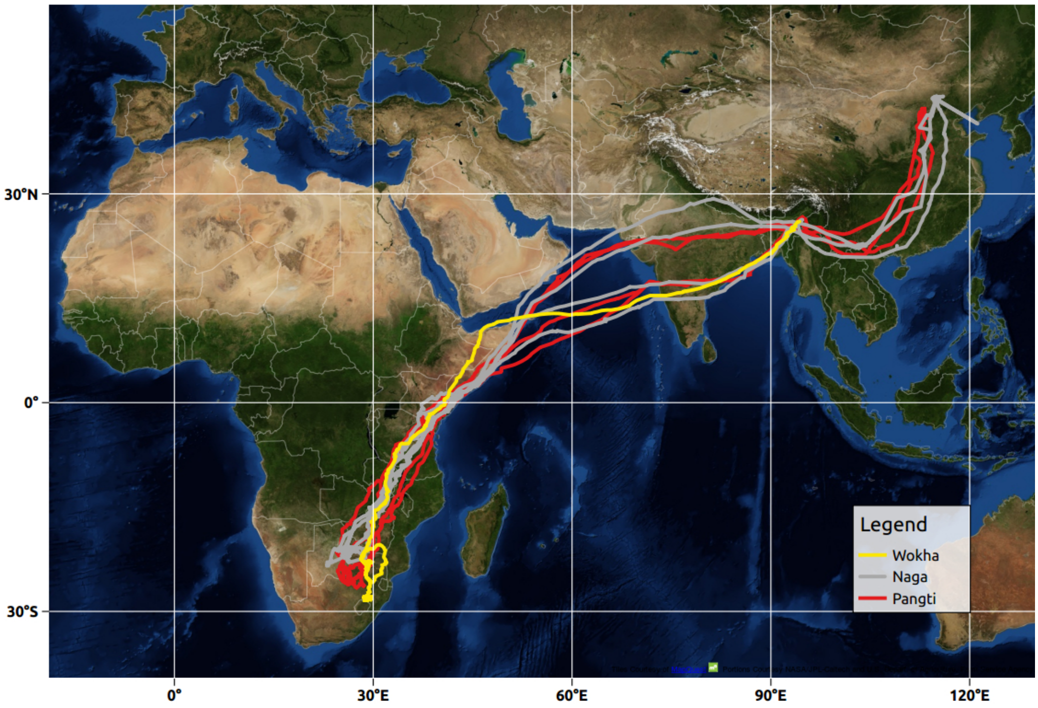

*Figure 1.1. Tracked trajectories of three Amur Falcons migrating from their northern Chinese breeding grounds to their southern African wintering grounds. These birds traverse half of the globe semi-annually crossing the Arabian Sea in a single, non-stop flight.*

Gulland et al., 2011) even if one would be carrying out observations at these locations. Migration strategies include, amongst others, nocturnal movements and/or high altitude flights, thus are often hidden from conventional techniques like observations or ringing. Moreover, these critical sites may be in remote parts of the world, especially on the Eurasian-African flyway, where carrying out conventional studies were and are still extremely demanding.

The iconic paper of Guisan and Zimmermann (2000) predicted the emergence of new, never before seen tools in both spatial data handling and statistical methodology that will enable researchers to infer on how the environment affects species. In case of avian distribution, habitat selection and breeding site selection modelling this prediction turned out to be true. With the exponentially increasing number of individual migratory trajectories of tracked birds, similar tools have been developed to link spatio-temporal environmental cues to decision making of individuals.

In my thesis I present a selection of studies that are connected through these methodological links. In Chapter 2 I describe species distribution modelling and how it can help nature conservation of a species identify key factors that may have led to demographic changes. Furthermore, I demonstrate that the power of spatial modelling can help identify and efficiently allocate active conservation measures in an area where resources are exiguous. In Chapter 3, I show how individual trajectories of long distant migrants can also contribute to better aid the localization of existing conservation efforts in the non-breeding

*Figure 1.2. Adult male and female Red-footed Falcons mating. Note the marked sexual dimorphism. Photo by Bence Máté.*

period. Furthermore I demonstrate that by overlaying large-scale, long-term environmental variables to individual trajectories of several species we have discovered a yet uncomprehended migratory barrier, and show how individuals cope when traversing it.

My thesis presents case studies already published or that are soon to be published. In case of published studies, I present them as published or with minor amendments that may help a more comprehensive understanding of the applied methods and obtained results.

My model species is the Red-footed Falcon (*Falco vespertinus Linnaeus* 1766). My fascination with these birds dates back to over a decade, and I have been lucky to find means to conduct several studies on these enigmatic small raptors.

### The Red-footed Falcon

The Red-footed Falcon belongs to the Falconidae family and the Falconiformes order. Being a monotypic species it's closest relative -which was once considered as a subspecies- is the Amur Falcon (*Falco amurensis*) breeding in East-Asia. (Cramp and Simmons, 1977; Ferguson-Lees and Christie, 2001) It is a small raptor; with a body size of 28–31 cm, and 65–75 cm wingspan. Adults weight 130–197 grams and demonstrate marked sexual dimorphism (Fig. 1.2). At least 3 age groups can also be distinguished based on plumage (juvenile, 2$^{nd}$ calendar year, adult).

The breeding range extends from Central and Eastern Europe to northern Central Asia (Fig. 1.3). The southern limit of the breeding range passes through Serbia, Bulgaria, Ukraine,

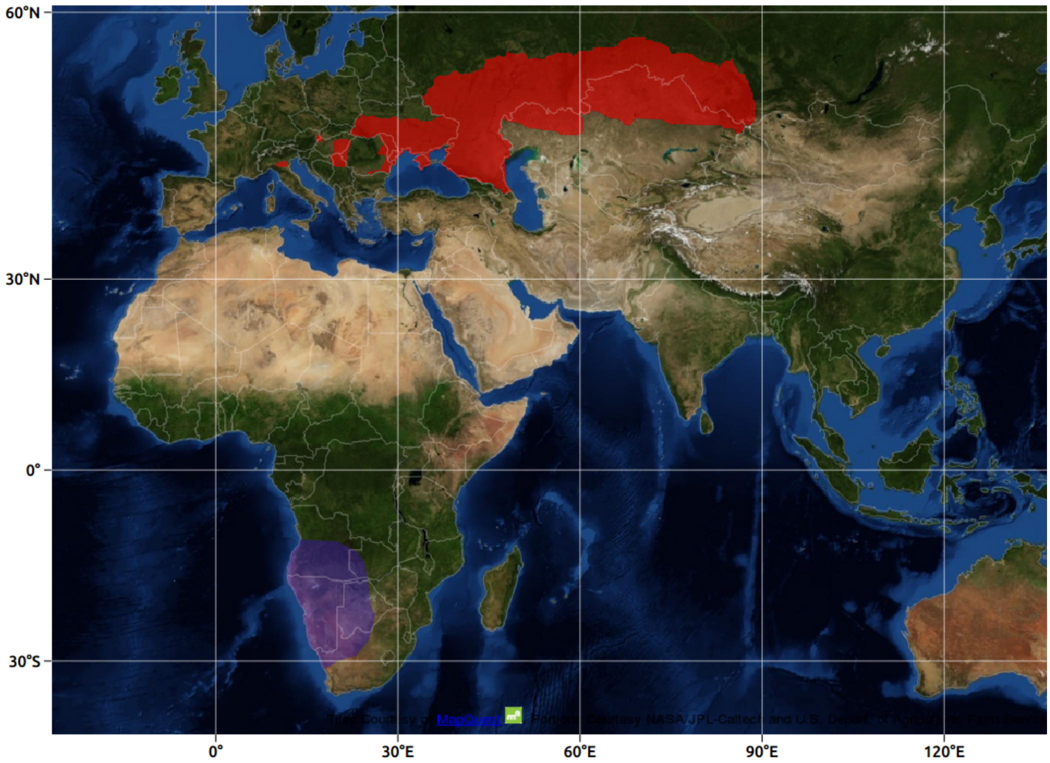

*Figure 1.3. Global distribution of the Red-footed Falcon (red: breeding, blue: core wintering range)*

Southern Russia and northern Kazakhstan (Cramp and Simmons, 1977; Purger, 2008). Irregularly breeding birds can be found northward to Belarus (Dombrovski and Ivanovski, 2005), western Russia north of Moscow, central Russia up to Novosibirsk, Krasnoyarsk and Khantia-Mansia region.

The core of the EU population breeds in the Carpathian Basin (eastern Austria, Hungary, western Romania, and northern Serbia) which form the western border of the range. A small but stable number of Red-footed Falcons breed in northern Italy (Sponza et al., 2001; Tinarelli, 1997). Occasionally, Red-footed Falcons may breed in small numbers in France (de Sousa, 1994; Pilard and Roy, 1994) and Finland. Vagrants were observed in most European countries (Dudley et al., 2006; Nightingale and Allsopp, 1994).

Red-footed Falcons are broad-front trans-equatorial migrants that fly individually or in loose groups, at various altitudes (Forsman, 1999; Leshem and Yom-Tov, 1996; Shirihai et al., 2000). The migration route of the European population is presumed to directly cross the Mediterranean, where birds are possibly utilizing mid-sea islands as stopover and roosting sites (Rossi and Bonacorsi, 1998; Roth, 2008; Shirihai et al., 2000). Pre-nuptial (spring) migration takes place between March and June, reaching Europe mainly in April/May up until the first half of June. Post-nuptial (autumn) migration takes place between August and late October. The species is highly gregarious during the breeding season, in the pre-migratory period and on migration.

The non-breeding range is found in Sub-Saharan Africa to South Africa; ranging from

*Figure 1.4. Typical Red-footed Falcon breeding site. Artificial nest-boxes and rook nests are both available for colonial breeding at this colony.*

*Figure 1.5. Adult male Red-footed Falcons engaging to occupy a nest-box in spring. Photo by Bence Máté.*

Angola and Namibia, through Botswana, Zimbabwe, Zambia to southern Kenya (Ferguson-Lees and Christie, 2001). Very few observations were recorded in South Africa despite of annual search efforts in the last 18 years (Anthony Van Zyl, Rina Pretorious pers. Comm.).

Red-footed Falcons prefer open habitats interspersed with small woods, groups of trees or shelter belts that provide nesting and roosting opportunities (Fig. 1.4). They inhabit steppe, pseudo-steppe, wooded steppe and extensive agricultural habitats, where they prefer crop mosaics with presence of fallow land, grasslands or alfalfa. In the Carpathian basin, stable colonies are formed close to grasslands. In Africa, they occupy grasslands, savannah and scrublands (Del Hoyo et al., 1992). The Red-footed Falcon is a facultative colonial breeder (i.e. breeding in colonies and in solitary pairs).As other falcons, this species does not build a nest, they occupy nests in Rook (*Corvus frugilegus*) colonies (rookeries) (Horváth et al., 2015; Kotymán et al., 2015; Horváth, 1956; Purger and Tepavcevic, 1999) or in loose aggregation of Magpie (*Pica pica*) nests (Végvári et al., 2001). Due to recent conservation actions aiming to compensate the lack of nesting sites in suitable habitats, the species started to breed in artificial nest-boxes colonies. In certain areas of the breeding range (e.g. in Hungary) over 60% (Fehérvári P. and Horváth É., 2015) of the population breeds in nest boxes (Fig. 1.5).

Solitary pairs occupy variety of nesting opportunities such as magpie nests, hooded crow nests (*Corvus corone cornix*), buzzard nests (Buteo sp.) as well as cavities in trees. Breeding in abandoned buildings - as in case of other small falcon species - has not been recorded yet, but some authors mention nesting on cliffs and ground (Del Hoyo et al., 1992).

*Figure 1.6. Colour ringed adult female feeding fledglings with one of the main prey items of the species, the field vole (Microtus arvalis). Photo by Bence Máté.*

The Red-footed Falcon is a generalist predator (Cramp and Simmons, 1977) the most frequent prey items are invertebrates, mainly Orthoptera, Odonata, Coleoptera (Haraszthy et al., 1994; Keve and Szijj, 1957; Purger, 1998). However, the majority of nestling food biomass during the breeding season is probably constituted by amphibians e.g. Spadefoot toads (*Pelobates fuscus*) and small mammals (Fig. 1.6) e.g. common vole (*Microtus arvalis*). Prey may be taken in mid-air, on the ground, from hovering or from a perch (Palatitz et al., 2011, 2015a). Typical perches are trees, fences, electric pylons or wires and also small lumps of soil.

For hunting they prefer low vegetation cover on grazed or mown grasslands. A three-year-long radio-telemetry based habitat use analysis showed that in the second half of the nestling period, Red-footed Falcons utilize agricultural fields (mainly alfalfa and cereal crops) more than previously anticipated, while inter-tilled crops are generally avoided (Palatitz et al., 2011, 2015a)

The clutch consists of 3–4 occasionally 5, reddish eggs laid, relatively late (May–June) compared to other raptors in the region (Fehérvári et al., 2015; Kotymán et al., 2015). Both parents take part in parental care. Although 2nd calendar year birds are considered mature, they seldom breed in their first breeding season. Reproductive performance was found to depend on ecological factors such as the annual variations of vole density and weather. (Fehérvári et al., 2011).

The Red-footed Falcon has a large global population estimated between 300,000-800,000 individuals (Ferguson-Lees and Christie, 2001), but recent evidence suggests that it is undergoing a large decline in certain parts of its range. The European population of 26,000-39,000 pairs suffered a large decline during 1970–1990 (Tucker and Heath, 1994), and has continued to decline during 1990–2000, particularly in the key populations in Russia and, with overall declines exceeding 30% in ten years. Recent data, collected for the European Species Action Plan estimated the total EU population below 3000 pairs, from which 40% breeds in Hungary (Palatitz et al., 2009) A national scale survey conducted in Ukraine in 2009, estimated an approximate decline of 23% compared to 1990–2000 (Kostenko, M. unpubl. report). Declines have been reported from eastern Siberia, where the species may have disappeared as a breeder from the Baikal region (Palatitz et al., 2009). In Hungary population estimates have shown a decline from 2,000–2,500 pairs in the late 1980s to 600–700 in 2003–2006, followed by a gradual increase to 1200–1300 pairs recently (Palatitz et al., 2015b). However, populations in central Asia appear to be stable, with the species reported as common in suitable habitats in Kazakhstan (especially in forest-steppe zone with rookeries), and no evidence of any population declines (Bragin, E. pers. com.). The marginal population in Italy is stable and/or fluctuating (Gustin et al. pers. com.).The Red-footed Falcon is a species of high international conservation concern (“near-threatened” in IUCN Red List, ANNEX I of European Commission’s Birds Directive 79/409/EEC) due to the drastic breeding population decline of the past decades (Palatitz et al., 2009). It is widely recognized that the loss of foraging habitats and/or breeding sites is predominantly responsible for the decrease in avian biodiversity (Gaston et al., 2003; Myers et al., 2000; Newton, 1994). Red-footed Falcons have suffered from both during the past decades as their hunting habitats have been altered (Burfield et al., 2004), while the drastic decrease in rookeries within the Carpathian Basin has had a serious impact on the available nesting sites. A conservation project (Conservation of *Falco vespertinus* in the Pannonian Region LIFE05 NAT/H/000122) has already developed a method to compensate for the lack of nesting sites by establishing artificial nest-box colonies in habitats thought to be suitable for these small birds of prey (Fehérvári et al., 2009). However, expert opinion, individual experience, anecdotic historical data and the protection status of the area had more roles in the designation of the location of these sites than verified scientific knowledge. The project’s monitoring scheme on the other hand later provided precise data on the spatial pattern and occupancy rate of these artificial nest sites.

# Chapter 2

# Breeding distribution modelling of Red-footed Falcons in the Carpathian Basin

## 2.1 General Introduction

Human-induced alteration of habitats is thought to be one of the key factors driving the decline of biodiversity. The loss and degradation of suitable habitats can be linked to the intensification of agriculture (Böhning-Gaese and Bauer, 1996) . Comprehending the relationship between environmental cues and habitat selection of individual species is of high priority from a conservation perspective. By revealing the governing dynamics of breeding habitat selection of a given taxa one may predict species viability, assess potential reasons for changes in distribution patterns, and predict current or future distributions. Due to the fact that Red-footed Falcons depend on rookeries and other corvid built nesting facilities, habitat degradation may have a complex effect on breeding habitat selection. The formation of rookeries, the density of magpies or hooded crows may correlate with certain environmental factors that may alter the breeding site choice of these species and thus shift that of the falcons. Red-footed Falcons are gregarious colonial breeders, thus the spatial distribution of breeding pairs is highly aggregated. Therefore, even minor alterations in habitats, or habitat choice of nest host species may have a considerable impact on substantial percentage of breeding pairs of a population. Moreover, the drastic shift in proportion of breeding pairs from natural breeding sites to nest-boxes also complicates the comprehension of breeding habitat choice, as the location of these man-made colonies were selectively chosen to suit anecdotal breeding site preference of Red-footed Falcons. Although these assumptions are seemingly correct, it is still vital to precisely understand the relationship between the environment and breeding habitat selection. In this chapter I detail two published accounts that help entangle these complex and confounding effects shaping the model species distribution. In the first study I demonstrate a potential explanation of the observed decline and shrinkage in distribution of Red-footed Falcons within Hungary. The second study can be considered as a continuation of the first paper, but in this case the revealed habitat-nesting site associations are used to predict where to allocate monitoring and various other active conservation measures, in a country with low funding for such initiatives.

## 2.2 Modelling habitat selection of the Red-footed Falcon (*Falco vespertinus*): a possible explanation of recent changes in breeding range within Hungary

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*Authors: Péter Fehérvári, Andrea Harnos, Dóra Neidert, Szabolcs Solt, Péter Palatitz*

### 2.2.1 Introduction

The analysis of habitat use and selection is important for adequate, well founded planning of species-specific conservation management (Pearce et al., 2008; Robles et al., 2007). Habitat selection and habitat use data are necessary for the prediction of a species' distribution (Araujo and New, 2007; Elith et al., 2006; Guisan and Thuiller, 2005), for the assessment of risk factors (Gröning et al., 2007; Xuezhi et al., 2008) drafting of habitat management regulations (Franco and Sutherland, 2004; Garcia et al., 2006) and for the conservation of a single species or a group of species. Habitat selection of birds of prey is a common research topic in conservation biology (Bustamante, 1997; Lopez-Lopez et al., 2007; Palomino and Carrascal, 2007; Toschik et al., 2006), since these birds are good environmental bioindicators (Newton, 1979; Roberge and Angelstam, 2004) and are often referred to as umbrella or flagship species (Ozaki et al., 2006; Sergio et al., 2006).

The Red-footed Falcon is an endangered colonial raptor species, with a continually diminishing population, classified as near threatened by the IUCN Red List (`http://www.iucnredlist.org/details/144562`). The breeding range is in open, typical steppe type habitats ranging from Eastern Europe to Lake Baikal in Central Asia (del Hoyo, 1994). This species is a long distance migrant, with presumed wintering grounds in South-Western Africa: from the Northern parts of the South African Republic through Namibia, Botswana, Angola, Zimbabwe and Zambia (Del Hoyo et al., 1992).

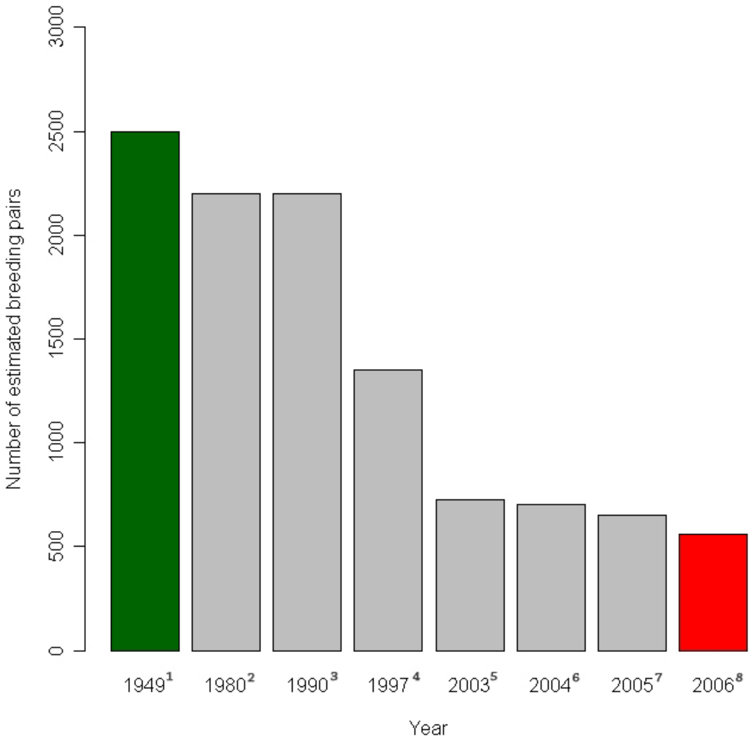

*Figure 2.1. The estimated maximum number of breeding Red-footed Falcon pairs in the past 60 years. The red and green columns reflect the number of breeding pairs of Fig. 2.3. and Fig. 2.2, respectively.*

*Source: [1]Keve and Szijj (1957),[2]Haraszthy (1981),[3]Haraszthy (1988),[4]Tóth and Marik (1999),[5]Haraszthy (1988),[6]Bagyura and Palatitz (2004),[7]Palatitz et al. (2005), [8]Palatitz et al. (2006)*

The territory of Hungary – which is the westernmost edge of the species' distribution range (Del Hoyo et al., 1992) – is almost negligible compared to its whole distribution area, but it has considerable importance in the conservation of this small bird of prey (Bagyura and Palatitz, 2004). Hungarian nature conservation has long focused on the protection of Red-footed Falcons, therefore the overall population estimates for the country are probably the most accurate throughout the global breeding range (Bagyura and Palatitz, 2004).

The first country-wide survey performed by Keve and Szijj (1957) in the middle of the last century estimated the breeding population to be 2200–2500 pairs, while the size of the population in 2006 was estimated at 500–600 pairs (Palatitz et al., 2006) .The methods used in these surveys differed markedly, therefore direct comparison cannot be made, but it is certainly true that the population had significantly decreased – possibly by up to 50% – during the past decades (Fig. 2.1).

Beyond the overall population decline, the spatial distribution of breeding birds was found to be radically different during the 2006 survey (Fig. 2.3) compared to

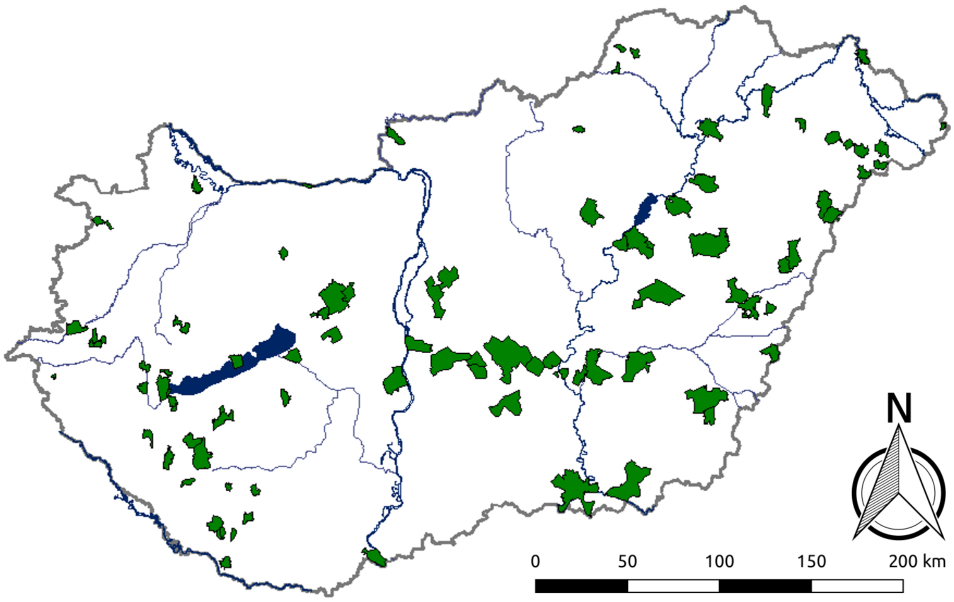

*Figure 2.2. Distribution of Red-footed Falcons in Hungary in 1949. Green polygons mark municipality borders where Red-footed Falcon breeding was recorded in rookeries*

1949 (Fig. 2.2). It is obvious that by 2006 Red-footed Falcons occupied almost exclusively the Great Plain region, practically deserting Transdanubia and Northern Hungary.

The conditions for the colonial nesting of Red-footed Falcons are primarily provided by rookeries (Horváth, 1964). The Rook used to be a wide-spread, common species from the 1940's (Vertse, 1943) to the 1980's (Kalotás, 1984; Kalotás and Nikodémusz, 1981), but as a consequence of an intensive eradication campaign in the mid 80's, the population rapidly decreased throughout the country (Kalotás, 1987) from about 260000 to almost 23000 pairs in approx. 30 years (Solt, 2008). In order to halt this trend, the Rook was declared protected by the Hungarian Nature Conservation Authorities in 2001.

As the result of the Rook population decline, the number of rookeries suitable for the colonial nesting of Red-footed Falcons also decreased. In order to compensate for this loss, artificial nest-box colonies have been established (Solt et al., 2005), (`www.falcoproject.eu`). Despite this large scale decrease in the number of breeding Rook pairs, rookeries are still available for Red-footed Falcon nesting throughout Hungary (Fig. 2.4). Red-footed Falcon population decrease therefore can, to some degree, be explained by the crash of the Rook population, but the recent changes in breeding range cannot. In this study we analysed the relationship between landscape scale habitat variables and the spatial distribution of colonies

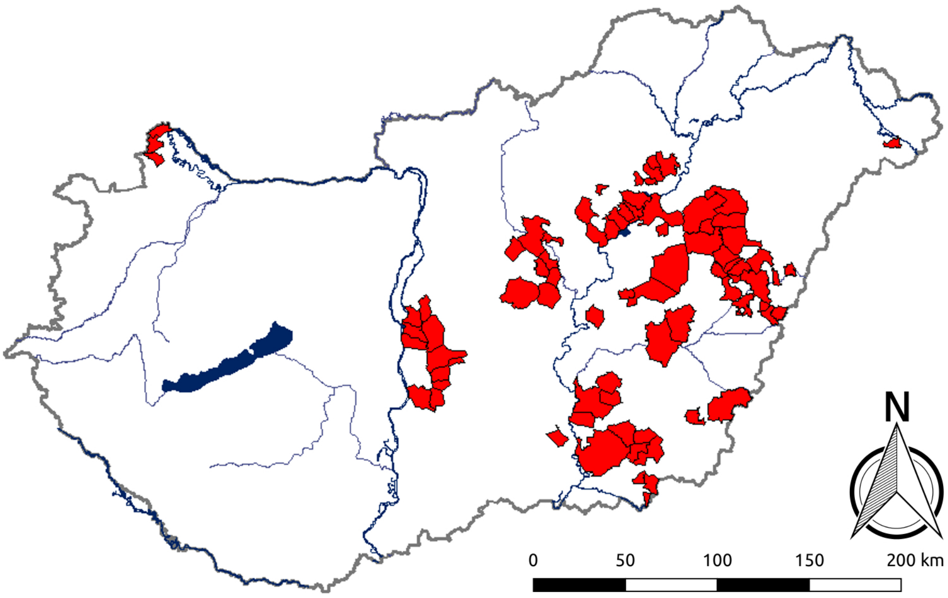

*Figure 2.3. Distribution of Red-footed Falcons in Hungary,2006. Red polygons mark municipality borders where within breeding pairs were recorded in colonies or as solitary pairs*

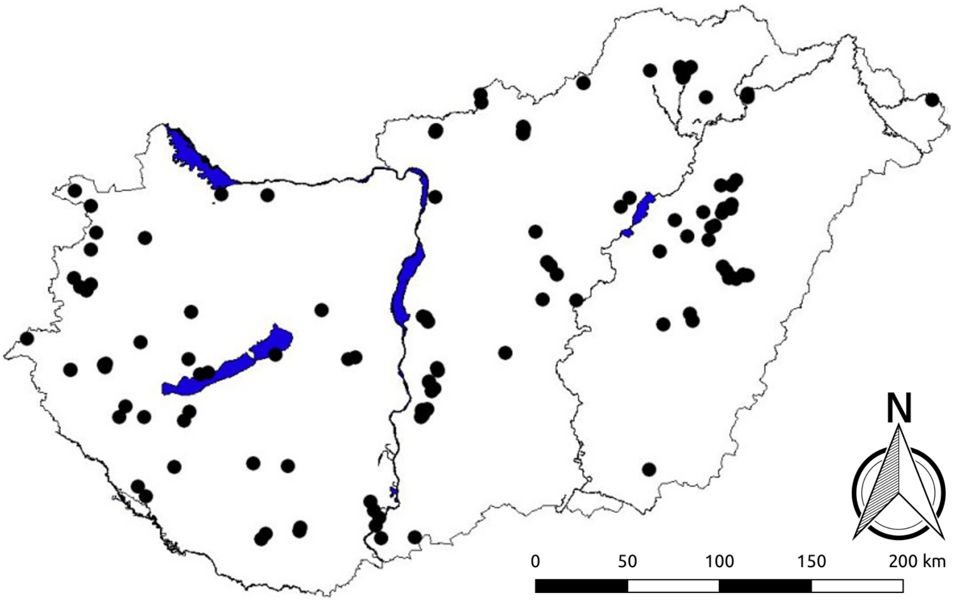

*Figure 2.4. Location of known rookeries in 2006. Despite the approx. 90% decline in the Rook population, the large scale distribution of rookeries was seemingly unaffected*

used by Red-footed Falcons in order to understand how these variables affect the current distribution pattern.

### 2.2.2 Materials and methods

As an initial step, we collected the coordinates of all colonies suitable for Red-footed Falcon breeding and defined the current breeding range in 2006. In the second stage we assessed the potential home-range of a Red-footed Falcon colony. This was carried out using habitat use analysis data deriving from a three year radio-telemetry study. The following step was to draw the potential home-ranges around the coordinates of every colony and to intersect these with a GIS database containing habitat describing variables. The variables within the potential home-ranges of every colony were later used for statistical modelling.

#### Data

The geographical coordinates of colonies derived from two separate databases: 1) the integrated population monitoring database of the Red-footed Falcon LIFE program, and 2) the database of Rare and Colonial Bird species of the Hungarian Ministry of Environment and Water (Solt, 2008). The analyses were carried out on two spatial scales. To be able to assess the differences between the 1949 (Fig. 2.3) and 2006 breeding distribution (Fig. 2.2) and to understand the pattern of colony occupation within the current breeding range, we spatially defined the ”historic” and ”current” breeding ranges.

We considered the whole area of Hungary as the ”historic” breeding range, because the 1949 distribution (Fig. 2.2) shows that there was at least one colony in every large region (apart from high altitude closed forests), therefore we did not a priori exclude any colonies based solely on its location. While the databases hold 198 potentially suitable colonies, we had to exclude the ones where the potential home-ranges protruded Hungary’s border. Therefore 162 colonies: 41 colonies with Red-footed Falcon presence and 121 without Red-footed Falcon presence were used in the analysis

The current breeding range was defined based on the municipality borders of Fig. 2.3 by applying a 500 meter buffer to the outline of the polygons and connecting the outer edges (Fig. 2.5). Two municipality borders (on the Northwestern and Northeastern part of the country) were excluded from the current breeding range because they held only four solitary pairs altogether. Therefore, the defined current breeding range holds all colonies occupied by Red-footed Falcons and over 99% of the solitary pairs.

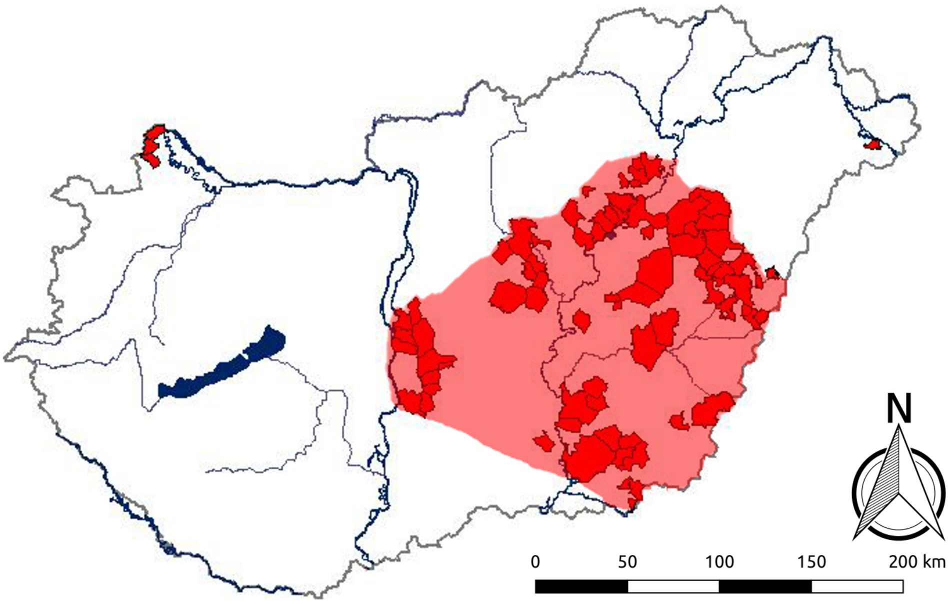

*Figure 2.5. Defining the "current" breeding range of Red-footed Falcons. The red polygons shown on the map mark the municipality borders where Red-footed Falcon breeding occurred in 2006 according to the monitoring data. The ruby red large polygon shows the area defined as the "current" breeding range in our analyses.*

### The potential home range of a colony

The true home-ranges of individual Red-footed Falcons were estimated from the data of the LIFE program's ongoing habitat preference analysis. We radio-tagged 24 birds in the 2006 and 2007 breeding seasons with 3.5 g "Biotrack TW-4" radio-tags. The birds were directly followed during their hunting, and the exact location of hunting events and other habitat use variables were recorded (see methods Franco et al. (2007); Tella et al. (1998)). To estimate the extent of potential home-range size of a given colony we created Minimum Convex Polygons (MCPs) using localization points of multiple tracked individuals breeding at the same colony. Although, the tracked birds may make long (4km) foraging bouts (Palatitz et al., 2011, 2015a) we estimated the potential home-range of a colony to be a 3000-meter radius circle, which covers at least 95% of the localization points of the studied colonies.

### Habitat variables

The habitat variables were extracted from the CORINE land cover frameworks GIS database. In Hungary, this database was created by SPOT4 Xi+M type satellite images shot in 1998 and 1999. The CORINE has 79 land cover categories that are used throughout Europe. The minimum area of uniform polygons is 4 ha. Although the database is relatively out of date, it is still usable to analyze certain variables due to its coarse resolution.

Out of the 79 existing variables we initially selected the ones present in the Hungarian landscape and later these were summed and transformed into 12 biologically relevant variables (Table 2.1). This aggregation of variables generally followed the CORINE level 1 nomenclature (Büttner et al., 2012) as shown in Table 2.1. The potential home-range size (3000-meter radius circles) was used to obtain the spatial explanatory variables surrounding each colony. We used the size, length and number of the habitat categories within the potential home-ranges for the analyses.

*Table 2.1. Spatial variables used to model landscape scale breeding colony occupancy of Red-footed Falcons. CORINE nomenclature codes show the original CORINE variable codes that where merged to form the used variable (see Büttner et al. (2012))*

| **Variable** | **CORINE nomenclature codes** | **Unit** |
|---|---|---|
| Water canals | 5.1.1. | meter |
| Forest | 2.4.4., 3.1.1., 3.1.2., 3.1.3., 3.2.4. | ha |
| River | 5.1.2. | ha |
| Road | 1.2.2. | meter |
| Grassland | 2.3.1., 3.2.1. | ha |
| Small parcel arable land | 2.1.3., 2.2.1., 2.2.2, 2.2.3., 2.4.2., | ha |
| Large parcel arable land | 2.1.1., 2.1.2., 2.4.1., 2.4.3. | ha |
| Farms | 1.1.1. (distant from settlements). | pcs |
| Settlements | 1.1.1., 1.1.2., 1.2.4., 1.3.1., 1.3.2., 1.3.3., 1.4.1., 1.4.2. | ha |
| Railroad | 1.2.2. | meter |
| Water surface | 5.1.2. | ha |
| Wetlands | 4.1.1., 4.1.2., 4.2.1., 4.2.2., 4.2.3. | ha |

### Statistics

We used Spatial Generalized Linear Mixed Models (Spatial GLMM) with logit link and binomial response to analyse the presence/absence of Red-footed Falcons in relation to landscape scaled habitat variables on both historic and current breeding range scales. A priori model selection was carried out using decision trees (Breiman et al., 1984). The advantage of decision trees is that, unlike to conventional modelling premises, there is no pre-defined relationship between response and explanatory variables, hence these models are less sensitive to missing data, to non-linear relationships and have the advantage to depict complicated hierarchical (high-order) interactions. We used a so called CART model (Classification and Regression Tree) which is a recursive partitioning algorithm. The general rule is to split the observations into two parts based on a predictor variable (root), then to split the subset further based on another or the same variable (categorical or numerical (De'ath and Fabricius, 2000; Elith et al., 2008)). The splits result in a node where data is partitioned into two groups, that are as homogeneous as possible. The algorithm then repeats the splitting procedure until pure homogeneous groups are found on the terminal nodes. These large ”overgrown” trees then have to be pruned back to a sensible size to allow inference on tree topology. In our case, the advantage of using CART models as means of variable selection was that the we could previously identify potential explanatory variables and explore their interactions prior to fitting sensitive linear models. Therefore, we only used the variables grouping the observations in CART models as explanatory variables in the Spatial GLMMs (Büttner et al., 2012). Decision tree pruning was carried out by optimizing the complexity parameter (Faraway, 2006). The CART models were unable to differentiate between artificial and natural colonies (decision tree, Cohen's $\kappa = 0.23$, 95% Confidence Interval:-0.02, 0.47), therefore we did not distinguish colony types in the analyses.

We used the QGIS sofware (Quantum, 2009) to handle and map GIS variables, and the R 2.6.0 sofware for data analysis (R Development Core Team, 2007). The most important R packages and their role in the analysis are presented in Table 2.2.

*Table 2.2. Most important R packages and their role used in the analyses*

| **Package** | **Role** | **Authors** |
|---|---|---|
| Adehabitat | Home range estimation | Calange |
| aspace | Measuring spatial distance | Remmel & Buliung |
| spdep | Measuring spatial autocorrelation | Bivand |
| mvpart | CART models | Therneau & Atkinson |
| MASS | Spatial GLMM | Venables & Ripley |

### 2.2.3 Results

**”Current” breeding range** The grouping variables of the decision tree applied on the current breeding range scale were: ”Forest”, ”Large parcel arable lands” and ”Grasslands”. The spatial GLMM fitted with these variables correctly classified 74 % of the observations (Cohen's $\kappa = 0.48$, 95% Confidence Interval: 0.3,0.67). The ”Large parcel arable land” variable had no significant effect, the ”Grassland” variable had marginally significant positive effect, while the ”Forest” variable had significantly negative effect, according to the model (Table 2.3).

*Table 2.3. The output of the spatial GLMM fitted on the presence/absence of Red-footed Falcons at a colony within the ”current” breeding range*

| | **estimate** | **SE** | **t-value** | **p-value** |
|---|---|---|---|---|
| Intercept | -1.37 | 1.53 | -0.89 | 0.3746 |
| Grassland | 0.03 | 0.019 | 1.68 | 0.0599 |
| Forest | -0.52 | 0.20 | -2.58 | **0.0164** |
| Large parcel arable lands | 0.013 | 0.019 | 1.01 | 0.4951 |

Although the ”Large parcel arable land” had a significant grouping effect in the decision tree, it turned out to be non-significant in the spatial GLMM. Presumably, decision trees overestimate the grouping effects of highly autocorrelated variables, hence the contradiction of the role of this variable in the different statistical analyses.

#### ”Historic” breeding range

The decision tree applied on the ”historic” breeding range scale (i.e. the whole country) classified 90% of the observations correctly. The grouping variables were: ”Roads”, ”Water surface”, ”Forest” and ”Grassland”. The spatial GLMM fitted with these variables classified 87% of observations correctly (Table 2.4). The classification of this model is also significantly deviating from random classification (Cohen’s $\kappa = 0.52$, 95% Confidence Interval: 0.51, 0.78). All grouping variables of the decision tree stayed significant in the spatial GLMM.

*Table 2.4. The output of the spatial GLMM fitted on the presence/absence of Red-footed Falcons at a colony within the ”historic” breeding range*

| | **estimate** | **SE** | **t-value** | **p-value** |
|---|---|---|---|---|
| Intercept | -3.33 | 1.16 | -2.87 | 0.005 |
| Forest | -1.5 | 0.33 | -4.52 | <0.001 |
| Grassland | 0.042 | 0.01 | 3.53 | <0.001 |
| Road | -0.19 | 0.085 | 2.21 | 0.023 |
| Water surface | -1.07 | 0.4 | -2.63 | 0.008 |

The significant ”Road” variable is highly correlated with the ratio of ”Settlement” variable (Spearman’s rank correlation coefficient = 0.75, <0.0001, therefore it can be used as an indicator of human presence. If the ”Settlement” variable occupied more than 25% percent of the potential home-range of a given colony, we classified it as

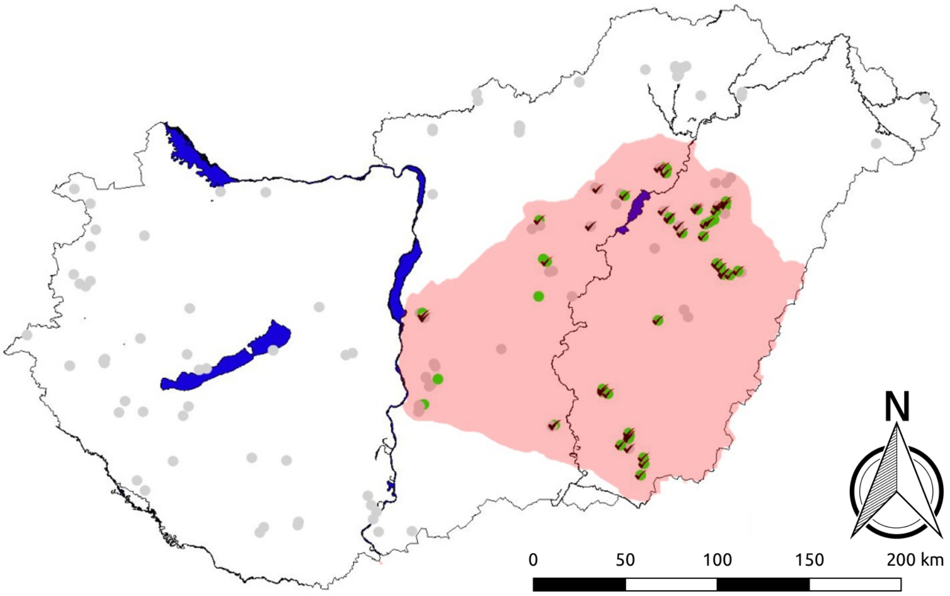

*Figure 2.6. The predictions of the historic breeding range model. According to our model predictions, there are no colonies suitable for Red-footed Falcon breeding outside the current breeding range*

urban colonies. Out of the 76 rookeries outside the current breeding range, 58 are classified as urban colonies. On the other hand, only 3 out of the 86 colonies within the current breeding range can be classified as urban colonies.

The ”Forest” variable had a negative effect on the probability of Red-footed Falcon presence at a given colony on both spatial scales, although there is a large difference in the ratio of forests between the two breeding ranges. The ”historic” model does not predict Red-footed Falcon presence at any of the colonies outside the current breeding range. (Fig. 2.6)

### 2.2.4 Discussion

Although the classification of the model fitted on the current breeding range is moderately accurate (74%), it reveals an interesting pattern in the case of the ”Forest” variable. This variable has significant negative effect on the probability of Red-footed Falcon presence in models fitted on both spatial scales, even though the variable range is quite different. The CORINE can only differentiate forest patches larger than 4 ha, therefore the 3% of forests in the potential home ranges of colonies within the current breeding range practically mean a few small patches or one larger patch. It is unlikely that the masking effect of forests at this scale (i.e. more forests mean less potential foraging areas like grasslands) is causing this observed avoidance pattern. However, the Goshawk (*Accipiter gentilis*) is a regular, well distributed (Haraszthy, 1988) predator of the Red-footed Falcons (pers. obs., Bagyura and Haraszthy (1994)), occupying small to large forest patches for breeding. Therefore, the observed colony occupying pattern of Red-footed Falcons can be explained as a predator avoiding strategy (e.g. Brodie Jr et al. (1991); Fontaine and Martin (2006)). The positive effect of grasslands was not as important as previously expected in the current breeding range model. Habitat use analyses revealed that this species uses agricultural lands relatively often for hunting (Palatitz et al., 2011, 2015a), suggesting that the birds can substitute grasslands to a certain degree, similar to Lesser Kestrels (Tella et al., 1998), causing the ”Grassland” variable’s lower explanatory power. The significant difference between colonies outside the current breeding range and the ones currently occupied by Red-footed Falcons can be explained by 1) the previously mentioned urbanization of Rooks outside the current breeding range, and 2) that the landscape has been significantly transformed over the past decades. (Source: Central Statistical Institute: `http://portal.ksh.hu/pls/ksh/docs/hun/agrar/html/tabl1_3_1.html.` Presumably, landscape modification has been greater outside the current breeding range, but most probably these two main causes acted synergistically to generate the current Red-footed Falcon breeding distribution. This presumption may be confirmed by the prediction map of the ”historic” breeding range model, which does not predict Red-footed Falcon occurrence outside the current breeding range (Fig. 2.6). Although our model variables derive from a coarse GIS database, and we only considered the distribution pattern of one year’s Red-footed Falcon breeding distribution, our model predictions may aid the mid-term nature conservation strategy of this near threatened species. It is quite clear that– in the current situation – without the local redistribution of rookeries (i.e. from urban to natural habitats outside the current breeding range of Red-footed Falcons) there is a low chance of Red-footed Falcon breeding range re-expansion.

## 2.3 Allocating active conservation measures using species distribution models: a case study of Red-footed Falcon breeding site management in the Carpathian Basin

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### 2.3.1 Introduction

The recent advancement in statistical sciences, geographical information systems (GIS) and the computing power available led to a boom in the number of modelling approaches available for species distribution modelling (Elith and Leathwick, 2009; Hirzel and Le Lay, 2008). These species distribution models (SDMs) are applied in an array of fields ranging from evolutionary perspectives (Titeux et al., 2007) to responses to climate change (Marini et al., 2009) and others (Guisan and Thuiller, 2005). SDMs can play a crucial role in identifying key sites for endangered species however are less often applied in conservation sciences compared to their relative potential (Engler et al., 2004; Parviainen et al., 2009; Wilson et al., 2010).

One of the most important challenges of modern nature conservation is to prioritize activities to allocate scarce funding and resources effectively (Brooks et al., 2006; Segan et al., 2010; Wilson et al., 2009). Increasing cost-effectiveness may be as simple as defining target areas where resources can be allocated. In case of certain rare, endangered and/or flagship species, major regional threats have already been assessed and methods to eliminate them developed (Heredia et al., 1996; Meyburg et al., 2001; Palatitz et al., 2009). Prioritization in these cases can be narrowed down to target areas based on various aspects like expert knowledge, expected conservation results or potential presence of the species in question(Bessa-Gomes and Petrucci-Fonseca, 2003; Olsson and Rogers, 2009; Yosef and Wineman, 2010; Zduniak and Yosef, 2012).

The Red-footed Falcon is a species of high international conservation concern (”near-threatened” in IUCN Red List, ANNEX I of European Commission’s Birds Directive 79/409/EEC) due to the drastic breeding population decline of the past decades (Palatitz et al., 2009). This small raptor is a facultative colonial breeder (i.e. breeding in colonies and in solitary pairs) that does not build a nest; falcons naturally breed in Rook colonies (rookeries, (Horváth, 1964; Purger and Tepavcevic, 1999) or in loose aggregations of magpie nests (Végvári et al., 2001).

It is widely recognized that the loss of foraging habitats and/or breeding sites is predominantly responsible for the decrease in avian biodiversity (Gaston et al., 2003;

Myers et al., 2000; Newton, 1994). Red-footed Falcons have suffered from both during the past decades as their foraging habitats have been altered (Burfield et al., 2004), while the drastic decrease in rookeries within the Carpathian Basin has had a serious impact on the available nesting sites. In Hungary, the landscape scale distribution of rookeries remained stable while the density and size of rookeries decreased and their location shifted to human settlements (Fehérvári et al., 2009) while similar patterns have been reported from other European countries (Orłowski and Czapulak, 2007). The reasons of Rookery declines can be attributed to a large scale persecution in the mid 80s, resulting in a massive 90% population crash. The obvious consequences for Red-footed Falcons was that most of the potential breeding colonies disappeared, causing a shrinkage in distribution range, and a decline in the number of breeding pairs (Fehérvári et al., 2009 and see references therein). Moreover, the ratio of solitary breeders increased, with only 40-50% of the whole population used colonies for breeding at the turn of the century (Bagyura and Palatitz, 2004).

A previous conservation project (Conservation of *Falco vespertinus* in the Pannonian Region LIFE05 NAT/H/000122) has already developed a method to compensate for the lack of nesting sites by establishing artificial nest box colonies in habitats thought to be optimal for the birds. However, individual experience, anecdotic historical data and the protection status of the area had more roles in the designation of the location of these sites than verified scientific knowledge. The project's monitoring scheme later provided precise data on the spatial pattern and occupancy rate of these artificial nest sites.

While Red-footed Falcon monitoring and conservation efforts have been implemented on a wide spatial scale in Hungary and in Romania, there is scant information on recent population trends, and distribution from Northern Serbia, where approximately 5-10% of the total EU population is thought to breed (Palatitz et al., 2009). However, reports of population decline and spatial distribution are available from the early 2000s (Purger, 2008). A recently initiated international project aimed to fill in the knowledge gaps by adapting the monitoring scheme and fund the implementation of conservation activities by placing 800 nest boxes for Red-footed Falcons in northern Serbia. The short duration of the project (15 month) hindered the implementation of a thorough Red-footed Falcon breeding site survey of the target areas, and thus designating the optimal sites for new colonies based on recent field experience was not feasible.

In the present study we focused on utilizing the vast and accurate data available on Red-footed Falcon distribution in Hungary and Western Romania, through assessing the landscape scale habitat preference of Red-footed Falcons with SDMs. Initially, we focused on understanding the relationship between landscape scale habitat variables and Red-footed Falcon presence. This information was later used to predict the presence of suitable potential nest sites in Northern Serbia, to identify target areas for surveying and to aid the designation of the location of artificial colonies.

### 2.3.2 Materials and Methods

#### Red-footed Falcon distribution

Red-footed Falcon distribution data was derived from the monitoring scheme, developed and first applied in Hungary and in Western Romania within the framework of the ”Conservation of *F. vespertinus* in the Pannonian Region” LIFE Nature program (`www.falcoproject.eu`). The monitoring concerns all nesting types i.e. natural colonies (rookeries, dense assemblages of magpie nests), artificial colonies, and solitary nests. In case of the latter two types the applied scheme allows to precisely estimate the number of breeding pairs. However, in case of rookeries typically presence/absence data are more reliable than the vague expert estimates given. Intuitively, there is also a considerable difference in the probability of discovering the location of Red-footed Falcon breeding sites considering the different nesting types. Obviously, the probability is close to 1 in case of artificial colonies, however in case of the other two types it is highly variable. Including artificial breeding sites in a distribution model may cause bias as the fact that breeding birds present at these nests is the product of human preconception of suitable habitats and the choice of the birds. The percentage of falcons breeding in natural nest sites during the study period was approximately 40% and 90% in Hungary and in Romania, respectively. This large deviation is due to the remarkably different number of rookeries on the two sides of the border. Our primary objective was to build models that can predict potential presence of the species (i.e. presence if nest sites are available or made available) and not to predict true presence. Simultaneously using the data from the two countries for model building allowed to estimate the broadest spectrum of potential nest-sites, regardless of the nest building species.

Additionally, there is a considerable difference in monitoring effort made in the two countries, as the number of participants is approximately 10-fold larger in Hungary. Thus, to avoid bias we used the presence only data of the location of all monitored nesting sites, regardless of the number of breeding birds. As the position of all breeding sites were measured with hand held GPSs, we considered the data accurate without any further adjustments. We used the data of all discovered sites between 2006–2009 in Hungary and in Western Romania.

The last large scale Red-footed Falcon survey in Serbia was conducted in 2000–2001 (Purger, 2008) though, sporadic data on breeding distribution is available from

2009–2010. The latter data in theory could be used to evaluate model predictions. However, the recent survey effort made is spatially biased, hence does not reflect the true distribution. Therefore, we only used the most recent data for illustration and confirmation of result outputs instead of incorporating them into the modelling procedure (Fig. 2.7).

*Table 2.5. Variables of the CORINE 2006 Land Cover project that were identified in the modelling area and thus used as predictors in case of all models. Level 1 and 3 refer to the original nomenclature of the CORINE 2006, * variables were left out of the models due to low variability*

| | | | Modelling area surface coverage | | Predicted area surface coverage | |
|---|---|---|---|---|---|---|
| Var. code | Name (level 3) | ACRONYM | Mean % | ±*range* | Mean % | ±*range* |
| 1.1.1. | Continuous urban fabric* | CONURB | 0.01 | *0.00–0.70* | 0.00 | *0.00–0.35* |
| 1.1.2. | Discontinuous urban fabric | DISURB | 4.57 | *0.00–32.84* | 5.04 | *0.00–46.16* |
| 1.2.1 | Industrial and comm. units | INDCOM | 0.70 | *0.00–9.21* | 0.52 | *0.00–10.29* |
| 1.2.4. | Airports | AIRPOR | 0.08 | *0.00–5.32* | 0.05 | *0.00–7.49* |
| 1.3.1. | Mineral extraction sites | MINEXT | 0.06 | *0.00–9.39* | 0.07 | *0.00–2.92* |
| 1.3.2. | Dump sites | DUMPST | 0.00 | *0.05–7.09* | 0.01 | *0.00–2.69* |
| 1.3.3. | Construction sites | CONSIT | 0.03 | *0.00–2.09* | 0.00 | *0.00–0.50* |
| 1.4.1. | Green urban areas | GREURB | 0.04 | *0.00–2.85* | 0.11 | *0.00–9.68* |
| 1.4.2. | Sport and leisure facilities | SPOLEI | 0.17 | *0.00–5.32* | 0.06 | *0.00–3.96* |
| 2.1.1. | Non-irrigated arable land | NONIRR | 65.16 | *2.51–98.98* | 70.00 | *0.30–99.44* |
| 2.1.3. | Rice fields | RICEFI | 0.26 | *0.00–18.51* | 0.00 | *0.00–0.00* |
| 2.2.1. | Vineyards | VINEYA | 1.25 | *0.00–47.85* | 0.20 | *0.00–18.30* |
| 2.2.2. | Fruit and berry plantations | FRUITS | 0.59 | *0.00–15.66* | 0.19 | *0.00–10.03* |
| 2.3.1. | Pastures | PASTUR | 8.79 | *0.00–43.81* | 2.50 | *0.00–24.17* |
| 2.4.2. | Complex cultivation | COMPLE | 2.29 | *0.00–43.69* | 5.51 | *0.00–35.38* |
| 2.4.3. | Agriculture – nat. veg.[a] | AGRNAT | 1.39 | *0.00–11.49* | 2.39 | *0.00–24.88* |
| 3.1.1. | Broad-leaved forests | BROLEA | 6.01 | *0.00–60.69* | 5.48 | *0.00–85.26* |
| 3.1.2. | Coniferous forests | CONFOR | 0.40 | *0.00–17.90* | 0.09 | *0.00–13.44* |
| 3.1.3. | Mixed forests | MIXFOR | 0.59 | *0.00–13.68* | 0.18 | *0.00–15.23* |
| 3.2.1. | Natural grasslands | NATGRA | 3.48 | *0.00–83.13* | 1.61 | *0.00–32.72* |
| 3.2.4. | Transitional woodland shrub | WOOSHR | 1.40 | *0.00–17.75* | 2.56 | *0.00–34.19* |
| 3.3.1. | Beaches dunes and sand plains* | BEASAN | 0.00 | *0.00–0.24* | 0.00 | *0.00–0.97* |
| 4.1.1. | Inland marshes | INMARS | 0.78 | *0.00–24.69* | 1.00 | *0.00–2.61* |
| 4.1.2. | Peat bogs | PEATBO | 0.07 | *0.00–13.98* | 0.00 | *0.00–0.00* |
| 5.1.1. | Water courses | WATCOU | 0.78 | *0.00–9.66* | 1.37 | *0.00–21.74* |
| 5.1.2. | Water bodies | WATBOD | 0.91 | *0.00–21.60* | 0.79 | *0.00–15.09* |

Var. code and Name (level 3) refers to the original nomenclature of the CORINE 2006. Variables indicated with an * variables left out of model buliding due to low variability.

[a] Land principally occupied by agriculture, with significant areas of natural vegetation.

### Land cover variables, modelling and predicted areas.

We used the CORINE 2006 Land Cover GIS data base (Corine Land Cover 2006- version 13 available from: `http://www.eea.europa.eu/data-and-maps/data/clc-2006-vector-data-version`), as this is the sole reliable source of information on the country-wide habitat composition in Serbia. The CORINE 2006 has a 1:100 000 scale, the minimum mapping unit is 25 ha and the minimum width of linear elements is 100m. The CORINE nomenclature consists of 44 different layer types describing the surface coverage. Twenty-nine of these variables were found in the modelling and predicted areas and were used as predictors in the models (Table 2.5).

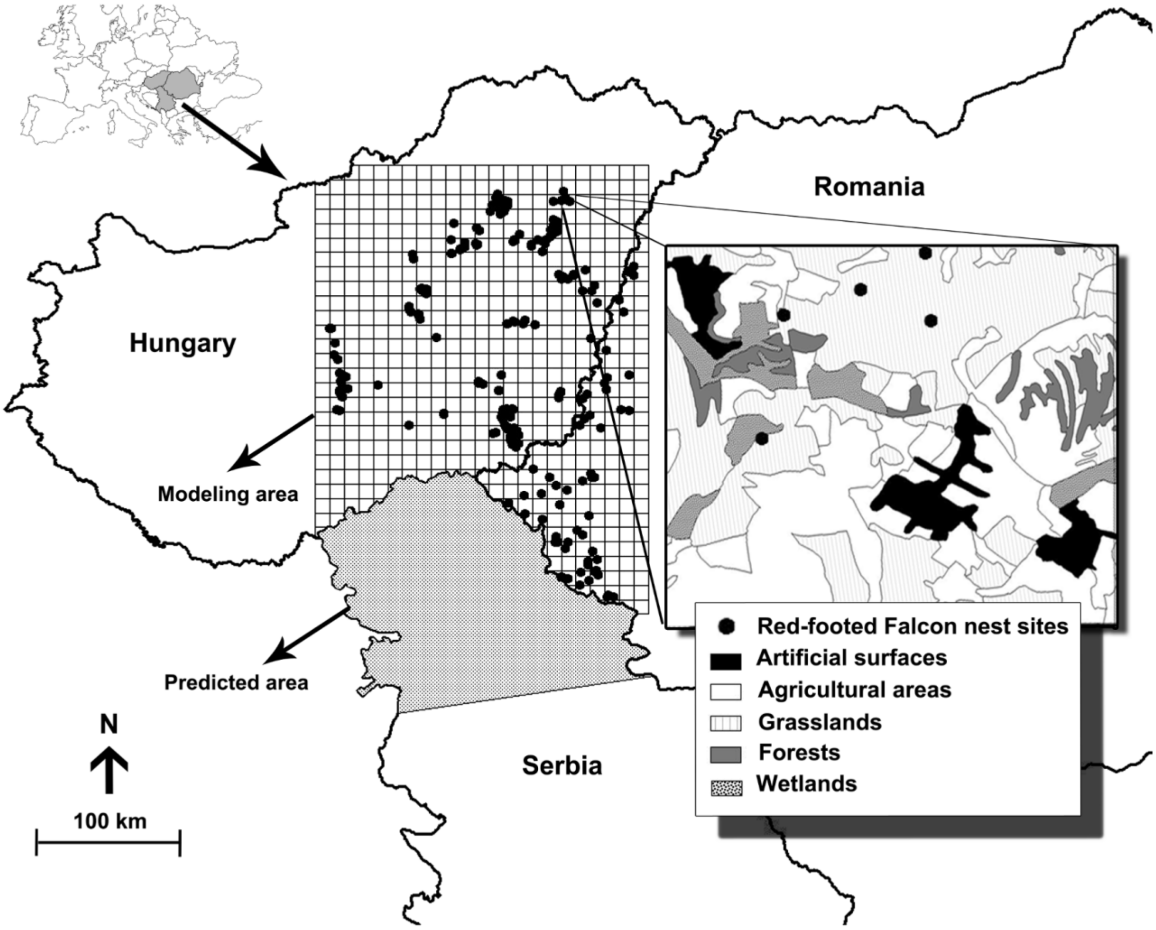

*Figure 2.7. Hungarian and western Romanian Red-footed Falcon distribution between 2006 and 2010 on a custom made 10x10 km grid system, the modelling area used in the analyses and the extent of the area used for model predictions. The modelling area was assessed so that the distance of the edges are 1 cell from the peripheral occupied cells. The predicted area is confined by the national borders of Serbia in the north, east and west, while the latitude of Belgrade was used as the southern limit. A sample of the habitat structure as defined by the CORINE 2006 of a given UTM cell is also presented. Level 1 grouping of CORINE variables (see Table 5.) was used, albeit natural grasslands and forests are depicted separately for clear visualization The sample habitat map of a given cell shows that the resolution of the variables used is relatively coarse. Note that the latter is only an illustration of the data, the actual distribution of Red-footed Falcon colonies in the depicted cell is not shown*

The fact that Red-footed Falcons have a 3–4 km diameter potential foraging area around a given colony (Palatitz et al., 2011), and that the resolution of the environmental variables is relatively coarse, led us to choose a considerably large 10x10 km grid scale for modelling. As a first step we created an arbitrary 10x10 km grid covering the whole Carpathian Basin. We then defined the modelling area as the smallest rectangle around the known breeding sites within Hungary and Western Romania. Where possible, a minimum of one cell distance was kept from all peripheral breeding sites to avoid edge effects (Ries et al., 2004) (Fig. 2.7). The prediction area for Serbia was defined as the area north of the latitude of Belgrade (Fig. 2.7). All habitat variables were clipped with the pre-defined grid and were transformed to their relative coverage within a given cell. The modelling area consisted of a 555 grid cells out of which 137 were identified as occupied, while the area to be predicted consisted of 277 cells.

### Model building

The impressive diversity of tools lately available for creating SDMs also yields considerable variance in model predictions, thus making the right choice of modelling procedure difficult for non-statisticians (Elith et al., 2006)(Elith et al., 2006). Thuiller (2003) proposed to use a framework of statistical approaches and to evaluate their relative performance on predicting a given species distribution before using them for novel predictions.

Machine Learning (ML) techniques are increasingly used as SDMs, because of their flexibility, robustness against outliers, non linear relationships and finally because they often outcompete conventional frequentist statistical models (Olden et al., 2008). In the current study we applied three ML techniques namely; feed-forward unsupervised Automated Neural Networks (ANN, Haykin (1994)), Generalized Boosting Models (GBM, Elith et al. (2008); Friedman (2001); Friedman and Meulman (2003)), and Random Forests (RF, Breiman (2001); Elith et al. (2006); Strobl et al. (2007); Svetnik et al. (2003)) together with Classification and Regression Trees (CART, Breiman et al. (1984); De'ath (2002); Hastie et al. (2005)) and Multivariate Adaptive Regression Splines (MARS, Friedman (1991); Leathwick et al. (2006); Munoz et al. (2004)) to describe the relationship between predictors and the distribution of Red-footed Falcons in the model area.

All models were applied simultaneously within the framework of BIOMOD (Thuiller et al., 2009) in the R software (R Development Core Team, 2011). Model accuracy was tested with splitting the data 10 times, using 70% of the observations in the modelling area in each random split (Araújo et al., 2005). In each run, the models' were evaluated on the remaining 30% of observations. The final run used 100% of the data in case of all models.

As our Red-footed Falcon distribution data was considered as presence only, we used randomly selected pseudo-absence data for modelling (Phillips et al., 2009). The scale of the study was set to that of the current distribution of the Red-footed Falcons in Hungary and in Western Romania (Fig. 2.7) therefore we considered that absence of the species from a given cell is of a random distribution, and that no other niche-limiting factors may have an influence. Thus, we chose a total of random 275 cells (approximately half of the modelling area) where no Red-footed Falcons were recorded as pseudo-absence cells. This randomization was carried out on three independent occasions and all models were run for all three sets with a total of 10 summing to a total of 165 models built altogether.

Selecting the best performing models was carried out using three methods; 1.) the area under the relative operating characteristic curve [AUC] (Hanley and McNeil, 1983; James and Barbara, 1982), 2.) Cohen's Kappa (Cohen, 1960), and 3.) the true skill statistic [TSS] (Allouche et al., 2006). The BIOMOD framework also allows for model comparison through a multiple cross validation procedure, which we have adopted to assess individual predictive power.

We used the randomization technique described by (Thuiller et al., 2009) to conclude variable importance in case of all models. This technique uses a model-independent approach allowing to make direct comparison of variable importance across the models. We also used evaluation strips (Elith et al., 2005) to determine the response curves of the three most influential variables.

Evaluating the probability of presence of nest sites in the predicted area was carried out by ensemble forecast of the two best performing models. The projected distributions were calculated with the weighted mean approach, using the cross-validation results to weigh predicted probabilities for a given grid cell (Marmion et al., 2009) The sensitivity-specificity sum maximization threshold (Jiguet et al., 2011; Liu et al., 2005) was used to transform model prediction probabilities to presence/absence predictions.

### 2.3.3 Results

Random Forests and Boosted Regression Trees proved to have the highest predictive power when considering the 3 runs with 100% of the data. These two models had the highest mean AUC values (0.98, and 0.94, respectively) and had the highest overall sensitivity and specificity values ranged across the threshold independent methods used for model evaluation (Fig. 2.8). Moreover, RFs were chosen as best models in 25% while GBMs in 21% of the model runs.

Both models agreed on the first three most influential variables namely; natural

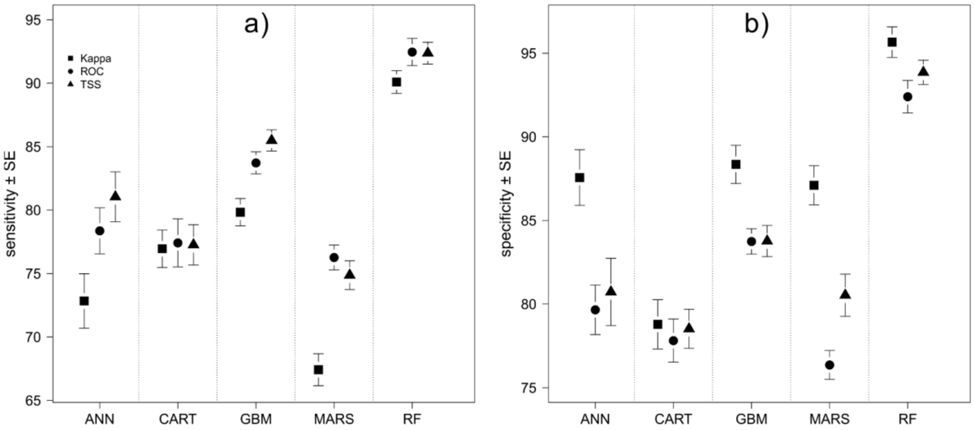

*Figure 2.8. Sensitivity and specificity of the 5 model types used in the analyses averaged across all three randomization procedures and all random splitting. a) Mean sensitivity values ±SE while b) mean specificity values ±SE as assessed by the Kappa, TSS and ROC and defined thresholds ($n = 33$, in case of all models). The probability thresholds were calculated to maximize the Kappa and TSS values and to maximize the percentage of correctly classified presences and absences in case of ROC, respectively. Random forests have the highest mean values in case of both sensitivity and specificity while GBMs show the second highest performance. The abbreviations of the x axis are; ANN: automated neural networks, CART: classification trees, GBM: generalized boosted regressions, MARS: multivariate adaptive regression splines, RF: random forests*

grasslands (NATGRA), broad leaved forests (BROLEA) and pastures (PASTUR) (Fig. 2.9). These variables were shown to have different effects on the probability of Red-footed Falcon nest-site presence (Fig. 2.10) The increase of natural grasslands and pastures had a positive effect on nest-site presence, while the increase of broad-leaved forests negatively influenced the probability of nest site-presence. Natural grasslands and pastures can be considered scarce and localized in both the modelling and predicted areas (Table 2.5) however are key to distinguish occupied and unoccupied cells in the modelling area.

The ensemble projection shows that in general, there is an east-west gradient in predicted probabilities with values on average higher in the northeast part of the predicted area (Fig. 2.11). When transformed to presence data, a total of 32 cells out of the 277 cells were predicted to have Red-footed Falcon nest-sites, which is 11.5% of the whole predicted area (Fig. 2.12). Moreover, the ensemble prediction of presence was 100% accurate in finding the currently known breeding sites (9 cells) in Northern Serbia.

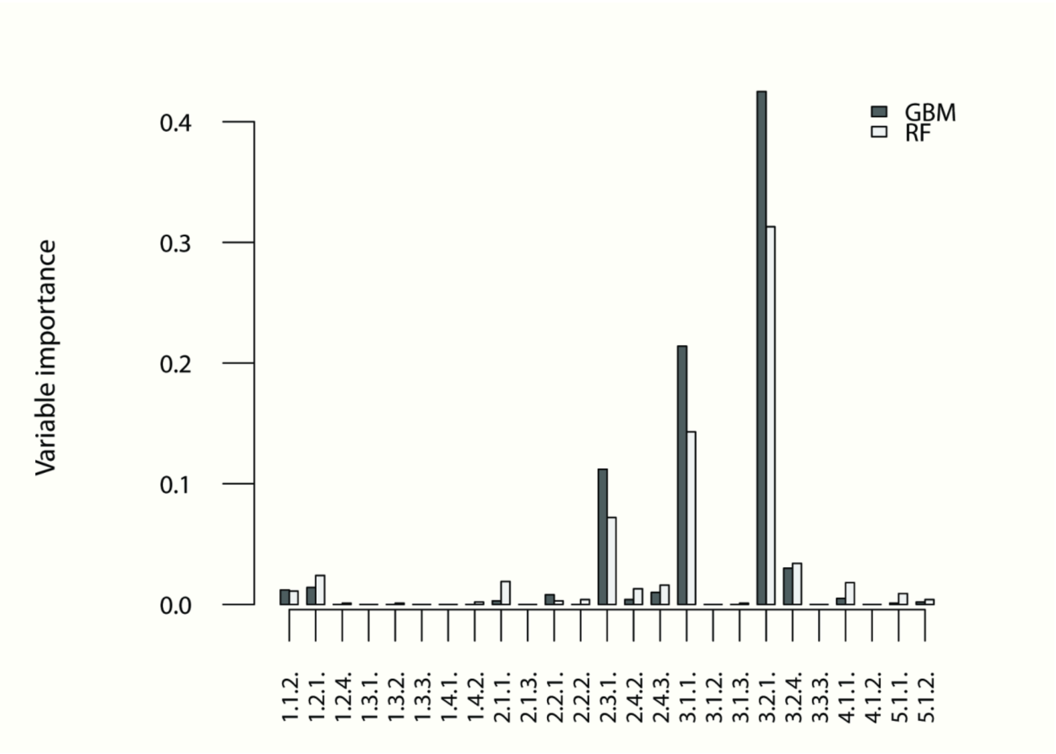

*Figure 2.9. Variable importance measures as defined by BIOMOD for RFs and GBMs. Natural grasslands (3.2.1.), broad-leaved forests (3.1.1.) and pastures (2.3.1.) have the highest importance measures compared to all predictors used in the models. For variable codes and names see Table 2.5*

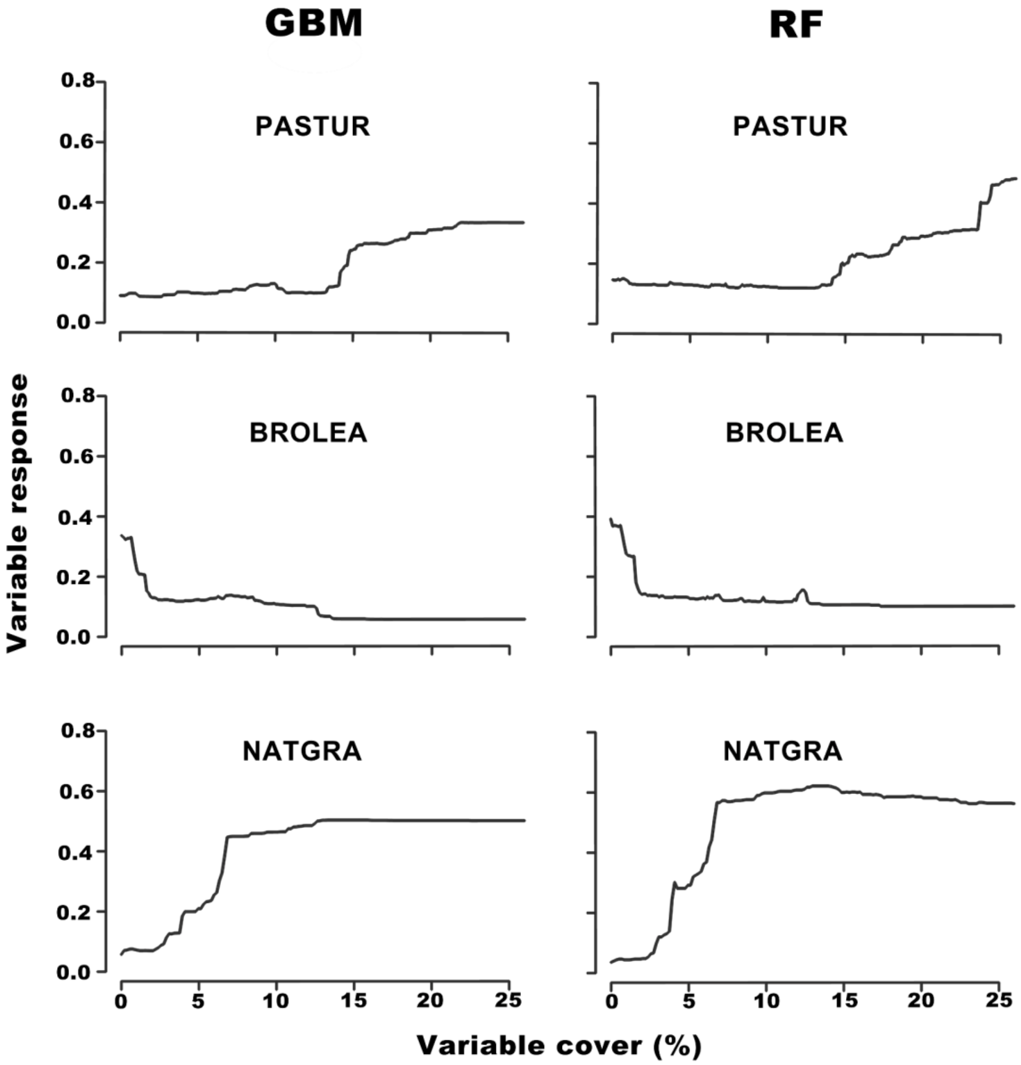

*Figure 2.10. Evaluation strips of the three most influential variables for RFs and GBMs. Prediction units are relative likelihoods scaled from 0 to 100. Both models agreed that natural grasslands (3.2.1.) and pastures (2.3.1.) have positive effect on the probability of Red-footed Falcon breeding site presence while broad-leaved forests (3.1.1.) have a negative impact*

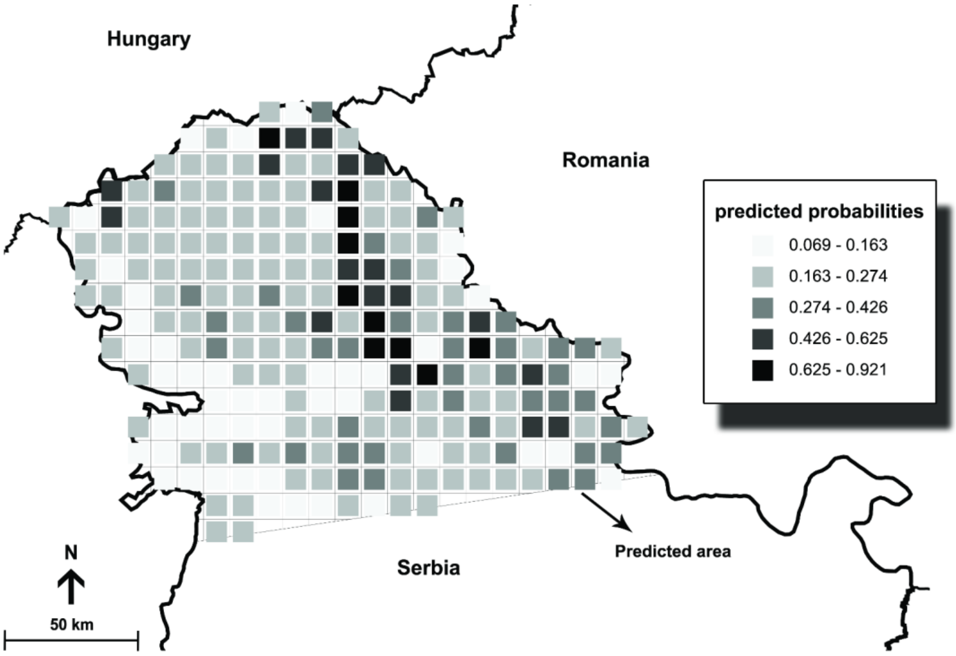

*Figure 2.11. Ensemble model prediction of probabilities of Red-footed Falcon nest site presence. There is a clear east-west gradient in the predicted probabilities*

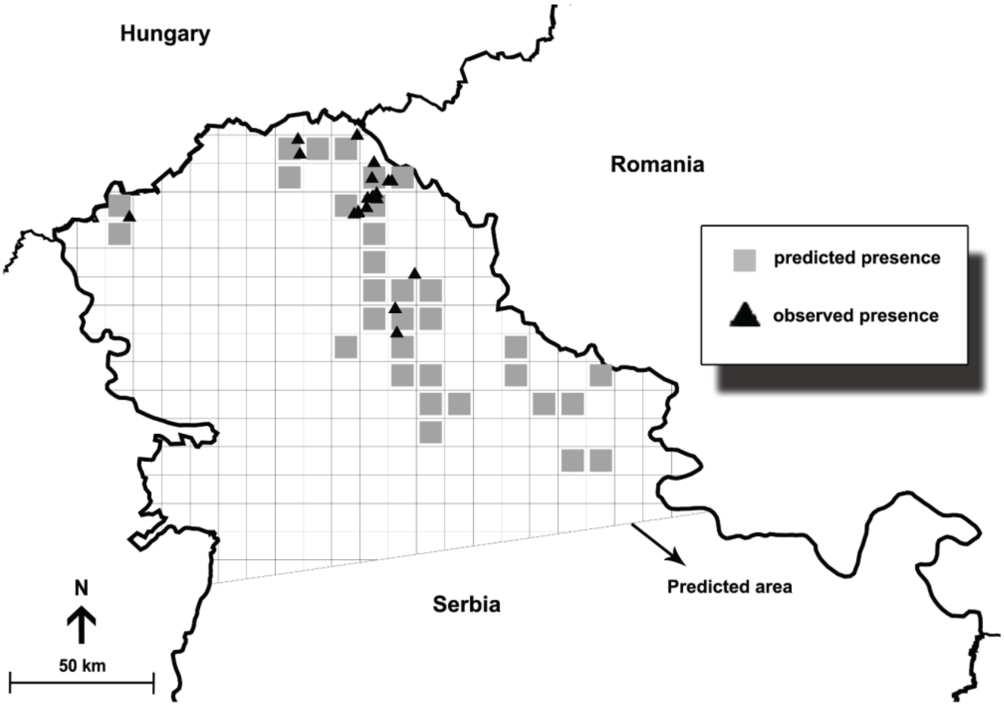

*Figure 2.12. Ensemble model prediction of presence of Red-footed Falcon nest sites. The model predictions classified 100% of the currently known (2009–2010) breeding sites correctly*

### 2.3.4 Discussion

**Landscape scale breeding habitat preference** Our modelling approach proved to be successful in describing the landscape scale habitat composition of Red-footed Falcon breeding sites in the modelling area. Both RFs and GBMs agreed that natural grasslands and pastures have a considerable impact on the probability of nest site presence, corroborating our previous findings from different spatial scales (Fehérvári et al., 2009).

The effect of natural grasslands and/or pastures is obvious in case of a steppe-species as these are most often utilized for foraging (Palatitz et al., 2011). On the other hand, the negative impact of broad-leaved forest may vary with the coverage percentage. Cells with vast forest coverage (15%) may be unsuitable for nesting due to low percentage of foraging habitats. The smallest mapping units of the predictors is 25 ha, thus any presence of forests in a given cell yields at least one larger homogeneous forest patch. These patches may be suitable breeding sites for Goshawks, a widespread raptor in both Hungary and Romania (Snow et al., 1998). Goshawks are also one of the handful of avian predators of Red-footed Falcons, thus the avoidance of cells with seemingly low forest coverage may be the result of a predator-avoidance strategy in nest-site selection (Fehérvári et al., 2009).

**Ensemble prediction of nest-sites**

There is increasing evidence that SDMs and their prediction in space and time may lead to erroneous conclusions if they are solely based on environmental predictors. For example, landscape scale decisions of breeding site choice may be influenced by the presence of intraguild predators (Sergio et al., 2007), or by non-environmental related behavioural traits of individuals (Penteriani et al., 2011). Moreover, habitat quality is not solely dependent of landscape structure, local/ regional conditions or land use may have a substantial part in shaping distribution patterns. For instance, Red-footed Falcon foraging habitat use is sensitive to vegetation cover that may be affected by environmental factors like precipitation or certain land use practices (Palatitz et al., 2011). The type and timing of different land use forms, especially in case of grasslands is governed by subsidy systems and regulations within the EU, however Serbia does not have a coherent legislative approach. Therefore, our results are to be treated with caution, and it has to be noted that they only resemble a possible scenario of potential distribution. Nonetheless, they present a solid backbone for designing and elaborating future conservation measures and allow to conclude important knowledge concerning distribution shaping effects.

The spatial pattern of predicted nest site presence probabilities (Fig. 2.11) shows a southwest-northeast gradient. This corroborates the lack of reported data from Srem County (Serbia), in the past decade (Purger, 2008). Once the predicted probabilities are translated to presence/absence predictions (Fig. 2.12), our findings resemble the spatial distribution of breeding sites in 1990–1991 (Purger, 1996, 2008). Grasslands, the main variables defining the current distribution in the modelling area, are scarce (1.6% mean coverage in the predicted area). Therefore, even small alterations in land use practices, especially converting grasslands to arable land, may have a drastic effect on the potential distribution. The predictions indicate that in theory, the landscape scale habitat structure has not limited the distribution of these falcons in the past two decades; hence the observed decline cannot be attributed directly to large scale changes in land use. However, in Serbia – where only a handful of artificial colonies exist to date – Red-footed Falcons are dependent on rookeries for colonial breeding. Red-footed Falcons are known to breed in rookeries found in the vicinity of, or in small villages in Romania, and Serbia. However, this is less likely in Hungary, probably because the traditionally widespread village pastures have been converted to arable land and/or industrial area. Presumably, urbanized rookeries in Hungary are often at a greater distance from the suitable foraging habitats. The distance of foraging grounds, thus the probability of finding prey within a unit of time, is thought to influence the viability of falcon colonies (Rodriguez et al., 2006). Rookeries may show a similar trend to urbanization in Serbia, thus the lack of rookeries may be one of the key factors to the observed Red-footed Falcon population decline. We therefore propose to survey predicted cells for Red-footed Falcon presence and for rookeries. We hypothesize that these areas are – at least on a landscape scale – suitable for Red-footed Falcon breeding and that nest site shortage rather than altered land use will be the primary cause of the lack of Red-footed Falcon breeding.

If proven true, the absence of nest sites can be managed with artificial colonies. However, the provisioning of nest boxes is only the first albeit probably a crucial step in conservation and there are a number of limitations to consider In general, Central European landscapes with high grassland proportions are scarce in trees suitable for rookeries and for installing nest-boxes. Our experience shows that the chosen trees for the artificial colonies have to fulfil at least three important criteria; 1) they have to be in the proximity of the foraging areas, 2) they have to be in suitable condition to be able to hold nest boxes for at least a decade and 3) they have to be less prone to illegal felling, a generally growing problem within the region (e.g. Purger (2008)).

None of the above mentioned factors were included in our modelling approach as there are no reliable, spatially defined data available for the predicted area. These aspects can only be assessed with regular visits, which have high labour and travel costs. Our results allow authorities and local NGOs to spatially weight conservation efforts focusing on areas with high predicted probabilities.

Serbia is a likely candidate for EU membership and as such has to fulfil nature conservation obligations like designating Natura 2000 sites. Red-footed Falcons can be considered as a classic umbrella species for eastern grassland habitats as they have an eminent role in the Natura 2000 designation process (`http://ec.europa.eu/environment/nature/natura2000/index_en.htm`). Therefore, locating their breeding sites or creating breeding sites by providing artificial colonies with the aid of our results has additional conservation and socio-economic benefits for both wildlife and the local human population.

# Chapter 3

# Non-breeding individual movement patterns

## 3.1 General Introduction

In this chapter I shift focus from breeding distribution and high level spatial statistics to the non-breeding period, tracked trajectories of individual falcons and common sense. The following case studies are based on 8 satellite-tagged (for details see methods below) Red-footed Falcons and their enigmatic journey through two continents in 2009/2010.

Prior to satellite tagging these falcons, there were only anecdotal and sporadic information on where and how this species migrates in non-breeding period. This lack of information was also assessed as one of the most important high priority threats in the European Species Action Plan compiled in 2009 (Palatitz et al., 2009). To have a rough estimate on migratory routes and wintering grounds of Red-footed Falcons initially, I compiled a database of all observations from birding trip reports, IBA atlases and country checklists for both Red-footed and Amur Falcons in all African countries (over 7000 trip reports scanned with approx. 700 records of both species) in 2007. I then classified each African country based on the frequency of observed individuals. The results of this unpublished data mining study were ambiguous as there was a large bias in observation effort between countries. Nonetheless, I could derive that, discarding small island nations, only 10 countries in Africa (including Madagascar) have no Red-footed Falcon records, while in the rest of the continent, at least sporadic observations were made (Fig. 3.1). General species monographs like the Handbook of the Birds of the World (Del Hoyo et al., 1992) depict Red-footed Falcon wintering area in south-western Africa, which is also corroborated by my results. However, the status of the species in West African countries like Mauritania, Senegal and Ivory Coast (Fig. 3.1) indicates that either not all Red-footed Falcons

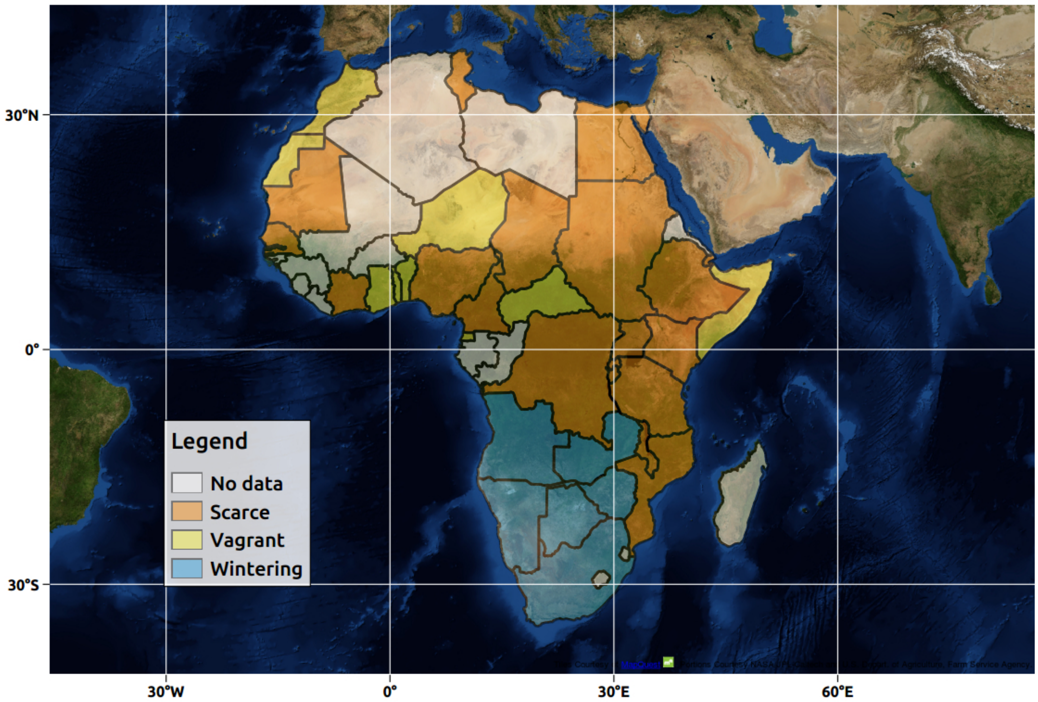

*Figure 3.1. Occurrence status of Red-footed Falcons in Africa from 2007. The information depicted is based on the IBA atlases, countrywide species check lists and trip reports of birdwatchers*

cross the equator for wintering and/or they may make substantial detours en route. The case of the Lesser Kestrels (*Falco naumanni*), a sister species that also migrates to Africa, shows how misleading incomplete information can be when it comes to identifying migration routes and wintering areas. Lesser Kestrels breed from the western Mediterranean region to Mongolia, and for long where thought to winter in southern Africa. A recent discovery of a large roost-site in Senegal and a set of follow up tracking studies (Catry et al., 2010) revealed that in fact this species has two spatially distinct wintering areas, one in southern Africa (Asian population), and one in Western Africa (Mediterranean population). I could not exclude that a similar scenario exists in case of Red-footed Falcons based solely on the countrywide status and observation report analyses.

However, the tracking of the 8 birds revealed a completely different scenario. The individuals that made it to the wintering grounds ($n = 6$) migrated on a broad front through the Mediterranean and the Sahara. In the Sahel region they oriented towards a specific area within the Congo Basin and flew over the rainforest zone of Africa (for detailed analyses of autumn migration routes see also (Lázár, 2013). The wintering area of these birds was within the water catchment area of the Okavango and Zambezi rivers (Fig. 3.2).

Identifying migratory routes and the wintering grounds of a high conservation value

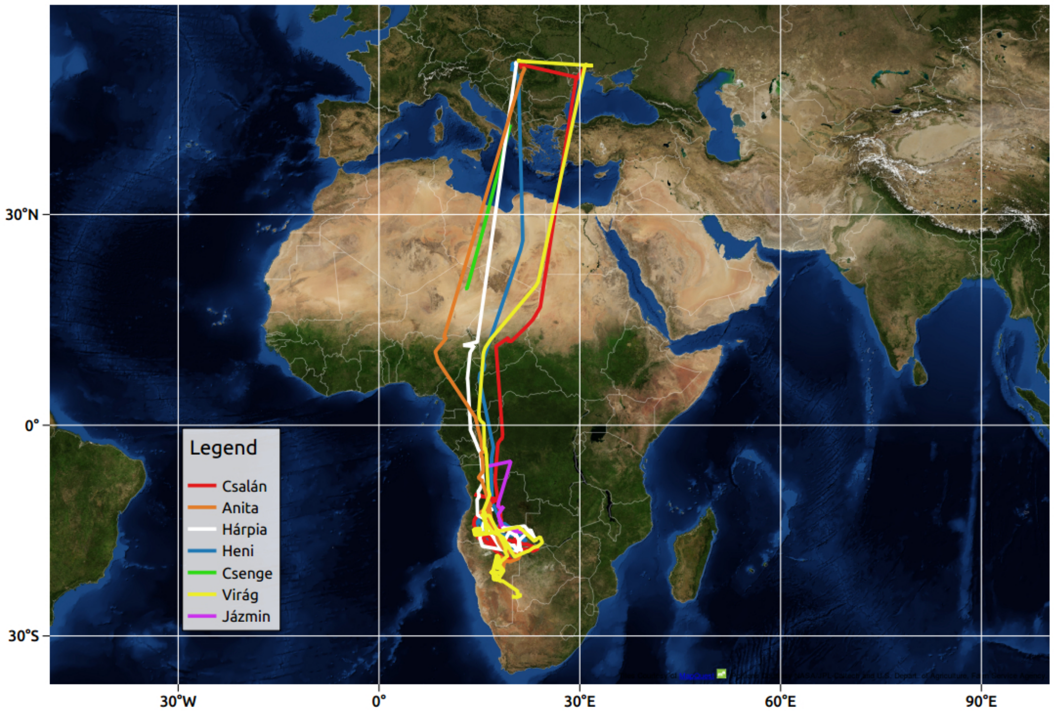

*Figure 3.2. Individual trajectories of all tracked Red-footed Falcons between 2009 summer and 2010 March. Out of 8 tagged individuals, we have at least partial data of 7 birds during this period*

species is in itself an important result. However, instead of merely reporting the general overview of routes, I demonstrate that in-depth analyses of individual migratory trajectories in specific time periods may provide direct conservation benefits and may shed light on processes shaping migratory routes.

## 3.2 Pre-migration roost site use and timing of post-nuptial migration of Red-footed Falcons (*Falco vespertinus*) revealed by satellite tracking

*Case study (as published in Ornis Hungarica 22(1): 36–47. 2014. Authors: Peter Fehérvári, Bence Lázár, Peter Palatitz, Szabolcs Solt, Attila Nagy, Mátyás Prommer, Károly Nagy, Andrea Harnos*

### 3.2.1 Introduction

Long-range migrant birds have precisely timed annual cycles that can be categorized into discrete periods, each having a considerable impact on individual life history (Alerstam and Lindström, 1990). Despite its presumable influence on survival, the pre-migration period – i.e. the period after breeding and before the commencement of autumn migration (Pagen et al., 2000; Rivera et al., 1999, 1998) – has been scarcely studied, mainly due to methodological restraints (de Frutos, 2008). Basically, this period may be utilized to optimize individual condition for migration, to select future breeding habitats and aid spring navigation (Mitchell et al., 2010). Several markedly differing behavioural patterns have evolved to achieve this goal. Dispersal from the natal breeding grounds is typical, but the magnitude of dispersion may be different amongst age and sex groups (Morton, 1992). Forming of large foraging flocks (e.g. Caccamise et al. (1983); Eiserer (1984); Metcalfe and Furness (1984) is not uncommon, and several species may also form common large roost-sites (Catry et al., 2010; De Frutos et al., 2007; Kruckenberg and Borbach-Jaene, 2004; Lambertucci et al., 2008; Newton, 1998). Intriguingly, only a handful of raptors breeding in the Western Palaearctic are known to form pre-migratory and wintering roost-sites (Ferguson-Lees and Christie, 2001). One of these is the Red-footed Falcon – a trans-equatorial migrant – of high nature conservation concern ("near-threatened" in IUCN Red List, ANNEX I of EC Birds directive 79/409/EEC, Annex I of the Bonn Convention). The core of the EU population breeds in the Carpathian Basin (Eastern Austria, Hungary, Western Romania and Northern Serbia) forming the western border of the range (Palatitz et al., 2009). Although they have long been recognized as facultative colonial breeders (Fehérvári et al., 2009a; Horváth, 1956), their autumn roosting behaviour has only recently been described in detail (Borbáth and Zalai, 2005). Today, a total of 20 stable roost sites (i.e. with birds present in every year since the discovery of the roost site) and 37 occasional (i.e. used in at least one year for more than one week in the period between 2004–2011) are known within the Carpathian Basin. These sites have been surveyed weekly (from mid August to early October) since 2006 in Hungary, Northern Serbia and Western Romania (Palatitz et al., 2010). Despite the extensive data on the spatial and temporal patterns on the number of birds present, little is known on the turnover rates and individual roost site selection. A single, second calendar year male marked with a VHF radio telemetry tag was shown to appear at several distinct roost sites in 2006 (Palatitz et al., 2011). This bird was the first to show the possibility of individual within-season movements between roosts (Fehérvári et al., 2007). However, there is no knowledge on the temporal and spatial dynamics of individual roost site use.

From a conservation perspective, being a gregarious in the post fledgling period makes large number of birds vulnerable to even small scale and/or local threats. The roost sites are often highly localized, found in a small group of trees, or even a single tree may suffice. In many cases, dirt roads are in the vicinity making unintentional disturbance probable. Other typical threats may be agricultural works, or felling of trees in the pre-migration period, but poaching has also been documented (Palatitz et al., 2009). Where the general protection against killing of the species is resolved, the roost sites can be conserved with relative ease. Active protection against disturbance and other threatening factors is needed only in short time period, and as these sites are highly localised, their protection hardly restrains large scale agricultural works or other human activities. Therefore, the knowledge of the location of roost sites is essential and often adequate for effective protection. Despite the fact that large, up to several thousand strong flocks may occur at a single site, it is remarkably challenging to find the exact location of the roost. Birds will approach the roosts in low light conditions often close to ground level and are less vocal compared to the breeding period (pers. obs.).

With agricultural intensification pacing up in Central and Eastern Europe, the conservation management of foraging areas surrounding the roost sites may also become important. However, effective measures can only be implemented if the spatial extent of foraging area and the habitat preferences are well established. Knowing the size of the hunting area may help understand the post-fledging biology and could aid designing specific large scale conservation measures (de Frutos, 2008).

In the current paper we used the data of 8 satellite tagged Red-footed Falcons to shed light on individual roost site selection patterns, the extent of individual foraging area and to locate new possible roost sites. The initial aim of deploying the tags was to reveal the autumn migratory routes and wintering grounds, however the data cumulated in the pre-migratory period will hopefully help in both elaborating direct conservation measures and reveal certain aspects of an important yet hardly known time period of an enigmatic raptor species.

### 3.2.2 Materials and Methods

#### Terminal Transmitter

We mist-netted 8 adult female-above average weighed- Red-footed Falcons and fitted them with 5 gram solar Argos Platform Terminal Transmitters (PTT-100, Microwave Telemetry Inc.) during the breeding season of 2009. The PTTs were harnessed on the back of the birds with a 5 millimetre Teflon ribbon (Kenward, 2001; Steenhof et al., 2006). At the time of harnessing, the 5g PTT was before mass production phase and it had not been widely tested. Initially, we observed that the tiny PTT may sink under the feathers and may cover the solar panels. We overcame the issue by applying small plastic ’slippers’ to lift the PTT out of the cover of the feathers. The whole mounting procedure was usually less than 45 minutes including all measurements and regular ringing activity. When possible, birds were revisited and followed for several days after tag deployment to ensure that the harness and the device is not altering their behaviour or flying capabilities. All birds were tagged at different breeding sites within the Carpathian Basin, seven in Hungary, and one in Western Romania.

The PTTs transmitted for 10 hours with 48 hour gaps in between two periods. When not transmitting, the device charged itself from the small solar panel on the surface. The transmitted signal was received via the ARGOS system and only location classes 3,2,1,0 were considered, A,B,Z were excluded due to low level of accuracy (Gschweng et al., 2008; López-López et al., 2009; Strandberg et al., 2009). In general,the reception of the signals by the Argos system is poor in Central Europe (in a circle of 1600 km radius around the Central Balkan with an approximately 1600 km radius), presumably due to the considerable background noise created by the numerous radio signal emitting devices like radars (Microwave Telemetry Inc. pers. comm.). Thus, bulk of the signals (79%) had to be excluded from the analyses, despite the fact that the pre-migration period is relatively long (mid-August to late September).

### Extent of foraging area around roost sites

We applied kernel home range estimate (Worton, 1989) on localization points that were obtained between 8 am and 6 pm during the whole pre-migration period. The smoothing parameter was calculated using the Least Square Cross Validation Technique (Seaman et al., 1999). Only a single individual provided sufficient number of high quality points ($n = 28$) to allow home-range estimation. We report a conservative (80%) kernel estimate of foraging area to avoid overestimating and to surely exclude data points that may derive from days when potentially a neighbouring roost site was visited.

It has to be noted that only a single individual's data was used in the analyses, thus the results are hardly representative of the population. We hypothesize that our results underestimate the extent of the true mean foraging area. Nonetheless the results presented rely on the best available data and allow to at least give a vague estimate that can be later used to fundament further studies (e.g. habitat use analyses) and active conservation measures.

### Locating potentially new roost sites

To identify yet unknown potential roost sites used by the tagged individuals we initially selected all localization points obtained between 9 pm and 6 am. We then applied a minimum convex polygon (MCP) in case of multiple data points close ($< 10$ km) to each other. Plotting these MCPs against known roost sites where tagged birds have been verified to spend the night allowed to estimate the general accuracy of obtained data. In some cases, the fitted MCPs did not cover the location of the known roost site, therefore we visually estimated the potential extent of an error buffer of 5 kms around the fitted MCPs. This error buffer seems to be relatively large, however the location of roost sites may slightly vary between years (Borbáth and Zalai, 2005). Our aim was to identify an area from where observers will have a good chance of spotting low flying birds towards the roosts, instead of trying to pinpoint the exact location of a potential new roost site. All buffered locations were then cross-referenced with the coordinates of all known roost sites. These coordinates derived from two separate sources; for roosts within the Carpathian Basin we used all roost locations that were found in 2006–2011, during the weekly pre-migration roost site surveys carried out in Hungary (Palatitz et al., 2010). We also used the data of a recent, yet unpublished country-wide breeding population survey carried out in the Ukraine (Kostenko, 2009).

### Assessing the frequency of roost site changes.

When possible, we used the evening locations described above to calculate the number of sites visited, and the number of times roost sites were changed by the tracked individuals. However, the large gap in transmission of the PTTs probably hindered the discovery of all roost sites used. To at least partially overcome this bias, we also considered the location points obtained during the day. In case an individual had a valid location point after 15 p.m. over approx. 200 km from the previous roost site, we considered that it spent the night at a different location.

### Migration Timing

We defined the commencement of migration when the tracked individuals initiated a non-returning southward movement. As the tracked birds are hardly representative of the whole population, we cross-referenced the timing of migration to that observed during the pre-migration roost site surveys. These surveys are carried out by professionals and volunteers on a weekly (32nd-40th week of the year) basis at all known roost sites in Hungary and at most known roost sites in Western Romania. Participants positioned in look-out spots estimate the number of birds entering the roost site. Less often early morning counts are also made.

All analyses were carried out using QGIS 1.7.3 'Wroclaw' (Quantum GIS Development Team, G. I. S., 2011), and R 2.13.1 (Calenge, 2006; R Development Core Team, 2011).

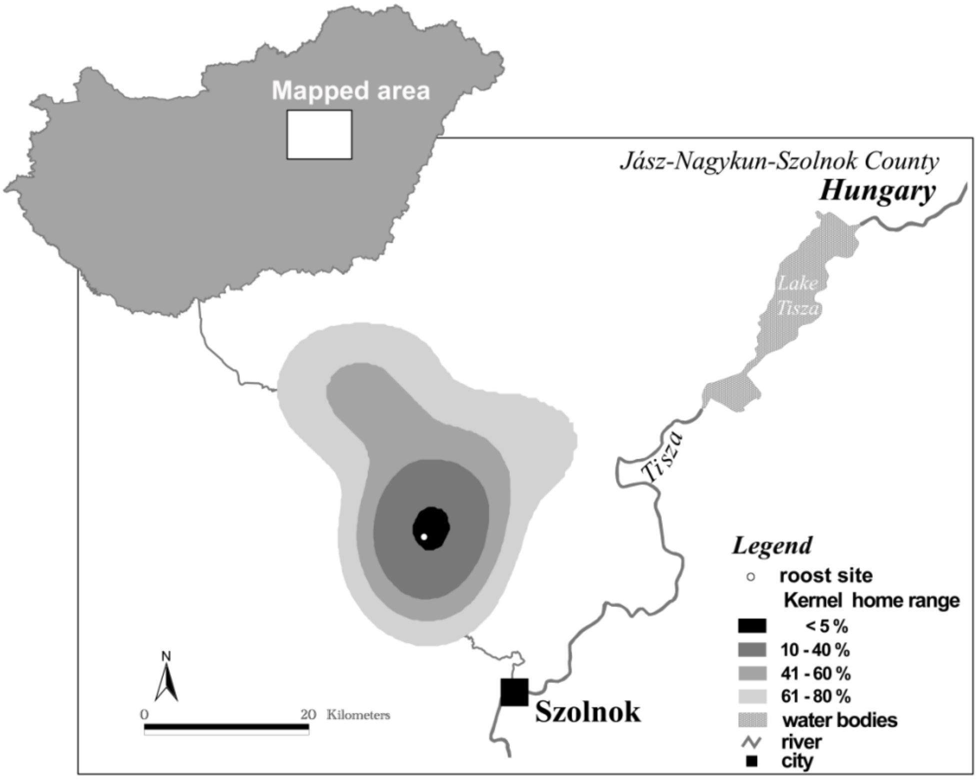

*Figure 3.3. Kernel home-range estimate of pre-migration foraging area extent of a single individual (Indiv. A) based on satellite localization points during the day. The 80% Kernel home-range (88 km$^2$) is highlighted and reported to allow conservative estimate of a foraging area extent and to exclude localization points deriving from days when the individual utilized a neighbouring roost site. The home-range is near concentrical, centring the roost site*

*Table 3.1. Number of roost sites used, number of times roost sites have been changed and the range difference of latitude and longitude of all coordinates obtained with PTTs of the 5 tracked birds. The first two parameters were calculated based on evening (between 9 pm and 6 am) locations, while the coordinate range differences were calculated based on all localization points. Birds spending their pre-migration period in the Ukraine seem to change roost sites more often, and utilize a larger area compared to individuals staying within the Carpathian Basin*

Fehérvári et. al

| ID | Nb. of roost sites used | Nb. of roost site changes | Latitude Range difference | Longitude Range difference |
|---|---|---|---|---|
| Indiv. A | 2 | 3 | 62 km | 101 km |
| Indiv. B | 1 | 0 | 38 km | 56 km |
| Indiv. C | 2 | 1 | 22 km | 110 km |
| Indiv. D* | 6 | 7 | 367 km | 214 km |
| Indiv. E* | 6 | 6 | 324 km | 609 km |

*Table 3.2. Location of identified potentially new Red-footed Falcon autumn roost sites*

| Country | Region/County | Latitude | Longitude |
|---|---|---|---|
| Hungary | Bács-Kiskun | 19.927 | 46.724 |
| Hungary | Hajdú-Bihar | 21.128 | 47.392 |
| Ukraine | Tatarbunarskyi | 29.986 | 45.815érvári et. al Ukraine |
| Ovidiopolskyi | 30.484 | 46.160 | |
| Ukraine | Berezivskyi | 30.883 | 47.415 |
| Ukraine | Novoodeskyi | 32.013 | 47.258 |
| Ukraine | Berislavskyi | 33.178 | 46.848 |

### 3.2.3 Results

A total of 5 of the 8 tagged individuals provided high quality localization points during the pre-migration period of 2009. In general we could show that most of the tracked individuals moved in between sites, only a single individual stayed in the vicinity of a single roost site (Table 3.1). The 80% kernel home range estimate of a single individual (Indiv. A) was 88 km$^2$ and was near concentrical around the roost site (Fig. 3.3).

Two tagged birds (Indiv. D, Indiv. E, see Table 3.1 and Fig. 3.4) left the Carpathian Basin and moved to southern Ukraine within days after PTT deployment, staying in the region until the onset of migration. The distance from the original trapping site to the first known roost site was 582 kms, and 657 kms for Indiv. D and Indiv. E, respectively. These two birds seemed to have changed roost sites more often, than

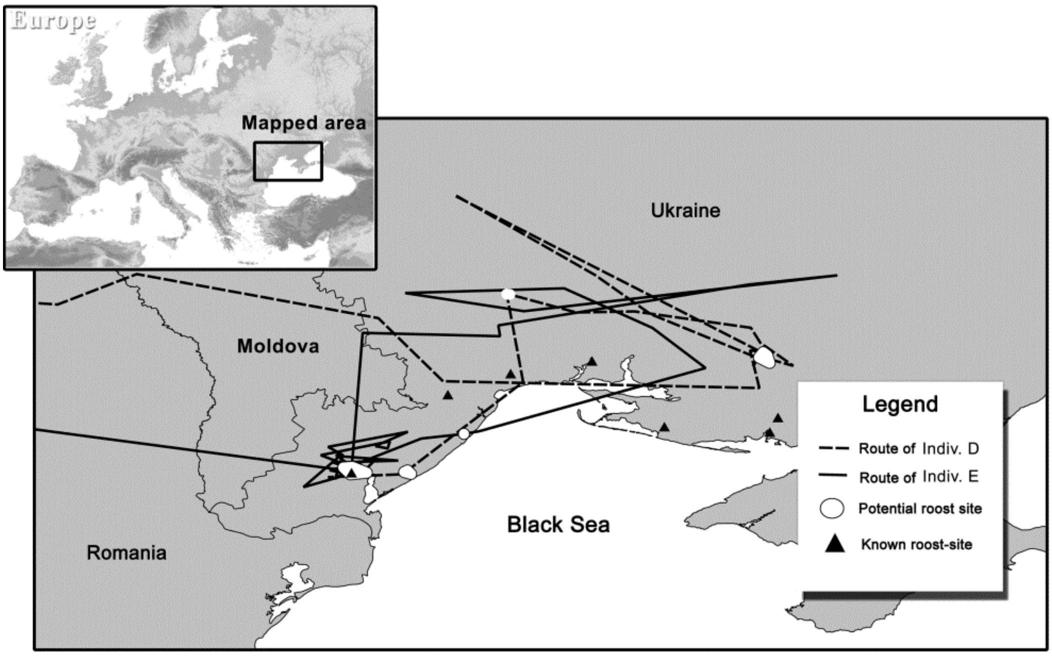

*Figure 3.4. Movement patterns and roost site usage of two tagged Red-footed Falcons spending the pre-migration period in the southern Ukraine. These two individuals seemed to be more prone to change roost sites compared to the individuals remaining in the Carpathian Basin, and also moved in a larger area. Their localization points also helped identify 5 new potential roost sites in the Ukraine*

those staying within the Carpathian Basin, and they have also moved in a larger area (Table 3.2). Only one of the seven known roosting sites in the Ukraine was used by these birds, however we were able to identify 5 new potential roost sites (Table 3.2, Fig. 3.4). We were also able to locate two new potential roost sites in Hungary (Table 3.1).

The timing of autumn migration of all tagged birds fell between the 37th and 38th week of the year (Fig. 3.5). When considering the change in the number of birds at the roost sites in the period between 2006–2011, the well visible decline (i.e. commencement of migration) fell between the 38th and 39th week, however a smaller proportion of the population is presumed to leave the pre-migration period a week earlier (Fig. 3.5). Roughly, the tagged birds departed together with the earliest individuals in the 37th week of the year.

### 3.2.4 Discussion

Our results suggest that Red-footed Falcon individuals may use multiple roost sites and that these roost sites may be separated by large distances. Intriguingly, birds may disperse to distant pre-migration sites – in our case to the northern Black Sea coastal region – even if potential barriers, like the Eastern Carpathians, stand in their

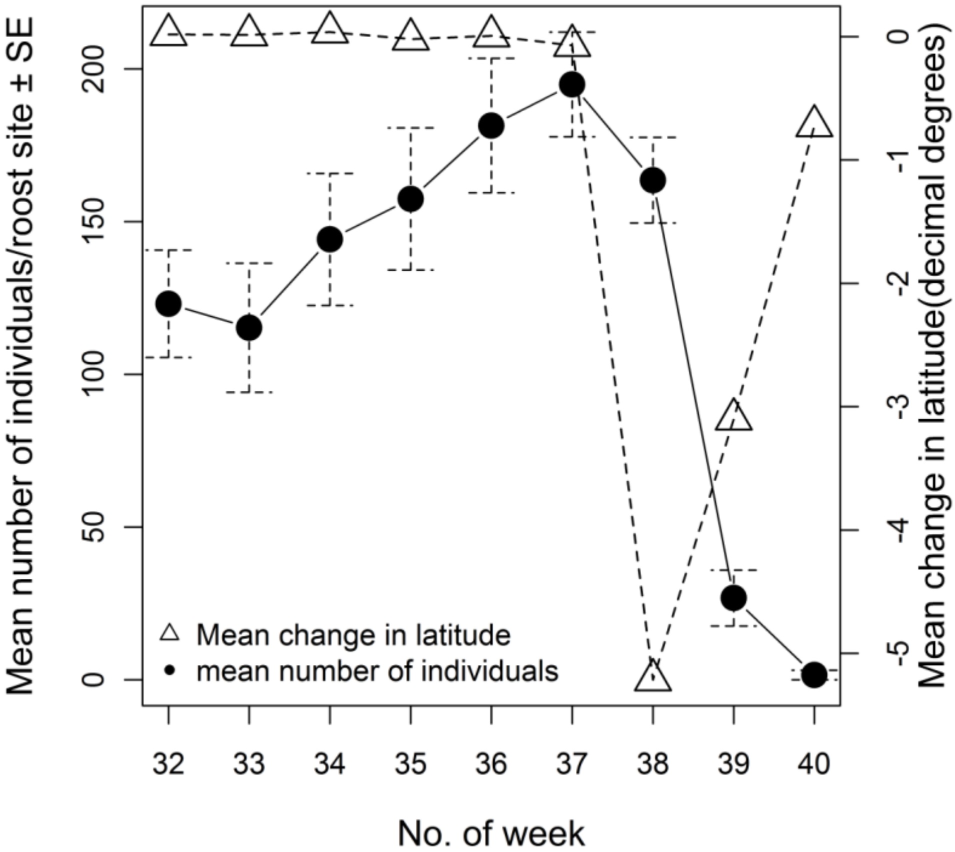

*Figure 3.5. Departure timing of satellite tagged Red-footed Falcons and temporal dynamics of the number of roost site using Red-footed Falcons. The first vertical axis refers to the mean number of individuals at the roost sites within the Carpathian Basin (2006–2011). The second vertical axis scales the relative change in mean latitude of consecutive localization points of the tagged individuals. The PTT tagged birds departed together with the earlier half of the population in between the 37th and 38th week of the year. Autumn migration is rapid, with the bulk of the population leaving the pre-migration roosts in a single week*

way. Moreover, tracked birds have been shown to change roost sites multiple times during the pre-migration period. The reasons of such a high mobility is yet unknown, we hypothesize that local weather and potential prey abundance may play a vital role in large scale movement decisions of these individuals. Red-footed Falcons often forage in flocks outside the breeding season, thus it might be possible that birds may get attracted to alter their roost site by joining a novel flock during the day.

Colour-ringed Red-footed Falcons from the Carpathian Basin have been re-sighted in Western and Northern Europe in autumn (Palatitz et al., 2009), however easterly movements have seldom been documented (Csörgő et al., 2009). For yet unknown reason the southern Ukraine seems to attract large number of Red-footed Falcons (Kostenko, 2009), including two of the tagged birds. These Red-footed Falcons may originate from the local breeding population and/or from birds of the Russian and Kazakh plains, and as our example shows there is a connection with the Carpathian Basin population. The tracked birds showed a somewhat different behaviour in the Ukraine, with more frequent roost site changes separated by larger distances. This seldom documented plasticity in pre-migration strategies may derive from individual differences or from different prey composition and habitat usage compared to that in Hungary.

It is important to note that the species is not legally protected in the Ukraine (Palatitz et al., 2009), making large number of birds vulnerable to hunting e.g. (BirdLife International, 2007). The lack of legislative background has recently been resolved as the Red-footed Falcon has been listed in Appendix I of the Bonn Convention (CMS) in November 2011. Thus, the Ukraine, as a full member of the CMS, is obliged to change the protection status of the species by 2014. However, the protection of roost sites is not so straight forward as they are most likely overlooked and their importance underestimated. An effective conservation measure against potential threats may be to encourage NGOs to maintain a constant monitoring of these sites. The participants monitoring may inform locals on the importance of the roost sites and report any potential threats. Our results may be used as reference points as the identified 5 new potential roost sites provide valuable information on the target areas worth searching.

Lesser Kestrels are close relatives of Red-footed Falcons and have similar life history traits (Cramp and Simmons, 1980). In Spain, the former species has been shown to use a mean of 350 ha of foraging area surrounding the roost sites (de Frutos, 2008), which is similar in extent to that used in the breeding period (Donázar et al., 1993; Franco et al., 2004; Tella et al., 1998). However, the foraging area extent estimated in our study was an order of magnitude larger compared to that in the breeding period (Palatitz et al., 2011). Moreover, Lesser Kestrels had high within-season roost fidelity, whereas the tagged Red-footed Falcons seem to be less constrained to a single site. All this may indicate that albeit these species are close relatives and are both highly gregarious throughout their life-cycle, the mechanisms driving the individual selection of a roosting site may be different. Red-footed Falcons leave the roosts at dawn and do not return until around dusk, therefore are less confined to the vicinity as in case of breeding. The reasons of a larger foraging area may be explained by increased intraspecific competition, as the number of individuals is larger at roost sites than in breeding colonies. Birds also lack the necessity to return to the site of origin after each successful hunt, thus can use larger foraging areas. A further plausible explanation may be that Red-footed Falcons alter their main prey source and/or their foraging habitat preference in the pre-migration period resulting in the observed pattern.

Our tracked birds have initiated their southward movements relatively early compared to the population. As the tagged individuals were chosen to be heavy, experienced adult females, this result is hardly surprising. However, interpreting the results has to be done with caution as two of the 6 departing individuals started their migration from southern Ukraine, from where no temporal data is available on the number of roosting birds. Nonetheless, all tagged falcons departed within the same week showing that global processes like photoperiod (Berthold, 1996) and/or regional weather (Shamoun-Baranes et al., 2006) may dictate their departure timing. Seemingly, the whole initiation of autumn migration is rapid, as over 90% of the birds disappear from the roost sites of the Carpathian Basin in two weeks, with the majority departing on the same week. Apart from potential foraging and anti-predatory advantages (Weatherhead, 1983), roosting may also be effective information sources to time departure for inexperienced juvenile birds. Cuing on conspecifics is not uncommon in social birds (Ahlering et al., 2010; Danchin et al., 2004) as public information may enhance the perception of resource quality of an individual. Red-footed Falcon roost sites may act as public information centres that allow assessing local mean foraging efficiency, predation risks and may also aid inexperienced migrants to adjust their departure decisions. Further suggesting this hypothesis is that most of the observations of Red-footed Falcons on migration are of small flocks instead of single individuals (Forsman, 1999). These birds migrate on a broad front (Ferguson-Lees and Christie, 2001) may utilize soaring, flapping flight (Shirihai et al., 2000) and may also migrate at night (unpublished data). Therefore, in theory are less confined to adjust departure decisions to weather, as in case of larger, soaring migrants. Thus, the gregarious behaviour en route may be deriving from common departure decisions at the roost site.

In conclusion, satellite telemetry of birds may not only provide insights on migration routes and wintering grounds, but may also help shed light on less known albeit important periods of individual life cycles. We present that even a small number of satellite tagged birds show behavioural plasticity in terms of roost site selection. Our results may help localize new potential roost sites, future conservation measures, and raise intriguing questions on individual decisions in the pre-migratory period.

## 3.3 Falcons reduce risk by migrating through corridors of predictable rainfall in the African rainforest

*Manuscript in prep.: Authors: Peter Fehérvári, Peter Palatitz, Szabolcs Solt, Andrea Harnos, Reuven Yosef, Richard H. Wagner*

### 3.3.1 Introduction

Avian migration routes are shaped by ecological barriers comprising vast areas of inhospitable habitats such as oceans, deserts, mountains and ice fields (Berthold, 1996). Whereas most of these barriers have been relatively well-studied (Strandberg et al., 2009), it remains unclear why tropical rainforests act as barriers. Birds traverse or circumnavigate rainforests in the Americas (Fuller et al., 1998; Kochert et al., 2011), Palearctic-African (Gschweng et al., 2008; Kassara et al., 2012; Strandberg et al., 2009) and Australasian migratory systems (Battley et al., 2011; Higuchi et al., 2005), indicating that rainforests present a challenge to a substantial proportion of migrating species. Rainforests are hypothesized to be unsuitable habitat due to a lack of foraging opportunities, high predation pressure (Berthold, 1996), or inhospitable weather (Strandberg et al., 2009). The Congo Basin is one of the wettest and most thunderstorm burdened areas of the world (Brooks et al., 2003), and should thus produce strong selection on migrants to either avoid the area or to develop coping mechanisms when crossing it. Evidence that the African rainforest acts as a barrier is that satellite-tracked Hobbies (*Falco subbuteo*) migrated through a corridor near it's narrowest section (Meyburg et al., 2011; Strandberg et al., 2009). However, data are lacking that would explain why rainforests comprise barriers to many migrants. Strandberg et al. (2009) suggested that among various factors, unfavourable weather conditions may cause rainforests to be barriers. This idea is supported by a satellite study of Eleonora's Falcons (*Falco eleonorae*), which in the context of ocean crossings suggested that migrants avoid areas of unstable meteorological conditions (Mellone et al., 2010). In this study we aim to investigate how individually tracked long-range migrant Red-footed Falcons respond to immediate weather conditions when crossing the rainforest zone of the Congo Basin. Furthermore, we considered published trajectories of two closely related species that also traverse the rainforest and examined how general long-term climatic parameters affect individual route choice.

### 3.3.2 Materials and Methods

#### Red-footed Falcon tracking

We mist-netted 8 adult female Red-footed Falcons and fitted them with 5 gram (approx. 3.5% of mean body mass) solar Argos Platform Terminal Transmitters (PTT-100, Microwave Telemetry Inc.) during the breeding season of 2009. All birds were tagged in breeding areas within an approximately 26,000 sq km rectangle within the Carpathian Basin, seven in Hungary, and one in Western Romania. The PTTs transmitted for 10 hours with 48 hour gaps in between two periods. The PTTs were harnessed on the back of the birds with a 5-millimetre teflon ribbons. The transmitted signals were received via the CLS/Service Argos system and only location classes 3,2,1,0 were considered, A,B,Z were excluded due to low level of accuracy (Gschweng et al., 2008). Five of the tagged birds had valid location points throughout the autumn migration period, while in case of the remaining three birds either the PTTs failed to communicate with the Argos satellites or presumably the individual died. One of the three birds started submitting after 2 months of deployment, south of the equatorial zone. We obtained a total of 3794 valid location points of the 5 analyzed birds between October and November 2009.

#### Red-footed Falcon route convergence

To assess whether the tracked trajectories converged non-randomly at a given location, we simulated random routes based on the observed trajectories, following the methods in Strandberg et al. (2009).

Briefly, the simulations were carried out by calculating the intersections of the estimated trajectories at every 5 degree latitudes between 40° N and 15° S, and randomly reshuffling these segments 1000 times for each individual. We then calculated the latitude-wise mean and the standard deviation of simulated values and compared them to the observed journeys. Probability values for random effects were estimated from the proportion of simulations giving the same or more extreme values as observed. We also ran separate simulations for two main parts of the journeys, 35° N–10° N and 10° N–10° S.

We found that overall latitude scatter of observed migration routes was significantly lower compared to the simulated null distributions (Table 3.3). Moreover, the latitudes of observed routes also deviated significantly from random. Considering the northern section of the migratory routes the observed scatter and mean latitudes was similar to that expected by chance, corresponding with the previous expected broad-front migration of Red-footed Falcons. However, the deviation in scatter and mean routes in the southern section (between longitude 10° N–10° S) showed a significant deviation from random routes, indicating that the funnelling of the tracked individuals was unlikely to occur by chance within the equatorial rainforest zone.

*Table 3.3. Results (p-values) of comparisons between observed migration parameters (mean longitude and scatter in longitude measured as standard deviation) and a set of 1,000 simulated random routes per tracked Red-footed Falcons. The scatter and means of observed routes deviated significantly from random throughout the autumn migration. When dissecting the routes and simulations to a Northern (35 °N – 10 °N) and a Southern (10 °N–10 °S) section, the results show that the scatter and mean longitudes of observed routes were similar to random in the first part of the journey, however both parameters showed significant deviation in the Southern section. The latter indicates a non-random selection of routes and that the observed birds converged in the equatorial region of Africa*

| | **Overall** | **35° N–10° N** | **10° N–10° S** |
|---|---|---|---|
| SD | 0.048 | 0.122 | <0.0001 |
| Mean | 0.008 | 0.06 | <0.0001 |

### Precipitation maps of Africa

We used the African Rain Fall Estimate RFE 2.0 of NOAA's Climate Prediction Center to produce the estimated spatial distribution of precipitation of Africa (`http://earlywarning.usgs.gov/fews/africa/index.php`). The RFE 2.0 has a resolution of 8 km and provides daily estimates of precipitation. To give a more concise presentation of the results we reduced the resolution of the data by applying a 3-pixel window neighbourhood-smoothing for all the obtained figures. In order to examine the locations of each falcon in the rainforest in relation to the spatial pattern of estimated rainfall, we used the dates of coordinates at (a) the starting point, i.e. the last recorded location point before the individual entered the rainforest, and (b) the date when the bird was located at the southern end of the rainforest. Since the location of the birds was known every approx. 68 hours (i.e. two 10 hours intervals plus a 48 hour gap), we used a maximum value of 3 days starting from the date of the last known coordinate north of the rainforest.

To assess long-term precipitation risk we initially calculated the median and median absolute deviation (MAD) for each pixel. The advantages of using these two parameters are that they are not sensitive to skewed distributions and outliers, while providing values similar to the mean and variance when distributions are symmetric, as is expected in long-term rainfall measurements.

We used the daily estimates from October and November because this is when the studied species migrated through the equatorial rainforest (Gschweng et al., 2008;

Kassara et al., 2012; López-López et al., 2010, 2009; Meyburg et al., 2011; Strandberg et al., 2009). Only pixels covering continental Africa were considered thus our maps rely on a total of 682*680600 8x8 km gridded rainfall estimates. Due to computational restrictions, we first calculated the median annual daily precipitation of all pixels of these months from 2001 to 2011 which is the interval for which the highest resolution data are available. We then calculated the 11 year median and MAD precipitation based on the annual values. Precipitation risk was calculated for each pixel as the product of overall median and MAD values.

#### Mean routes of Hobbies and Eleonora's Falcons

We used the maps of autumn migration trajectories and other published information to assess approximate extent of migratory flyways (Gschweng et al., 2008; Kassara et al., 2012; López-López et al., 2010, 2009; Meyburg et al., 2011; Strandberg et al., 2009) for Hobbies and Eleonora's Falcons. For Hobbies, we used the Fig. 24 published in Strandberg et al. (2009) and Fig. 25 of Meyburg et al. (2011) to redraw the mean routes. In case of Eleonora's Falcons we geo-referenced high resolution versions of the published figures based on features that could be localized accurately (e.g. the center of Sao Tomé and Principié, the tip of the Eastern Horn of Africa) and interpolated the localized points and routes. We applied this technique successfully before for re-analysing published accounts of distribution maps (Vas et al., 2013). Mean routes were calculated as the mean latitude for every second degree longitude between longitudes 10° N and 10° S). This procedure was performed twice, for Eleonora's Falcons that entered the rainforest and for those that circumvented it. All described analyses were carried out using R 2.14.2 (R Core Team, 2013), GRASS 6.4 (GRASS Development Team, 2012), and Quantum GIS 1.8.0. (Quantum GIS Development Team, 2013).

### 3.3.3 Results and Discussion

Here we present the first empirical evidence to our knowledge that rainforests comprise barriers because of stochastic dense precipitation. We found that the trajectories of satellite-tagged Red-footed Falcons significantly converged (Fig. 3.6, Table 3.3) in the Congo Basin rainforest, at a similar location as the trajectories of the Hobbies. We examined their short-term movements in relation to the locations of dense precipitation. All five falcons avoided rainfall and did so by either crossing on low precipitation days (Fig. 3.7 A), suspending southward movement amid heavy rainfall (Fig. 3.7 C1,C2) or circumnavigating localized rain concentrations (Fig. 3.7 B,D,E). These avoidance tactics caused the falcons to substantially increase their travel dis-

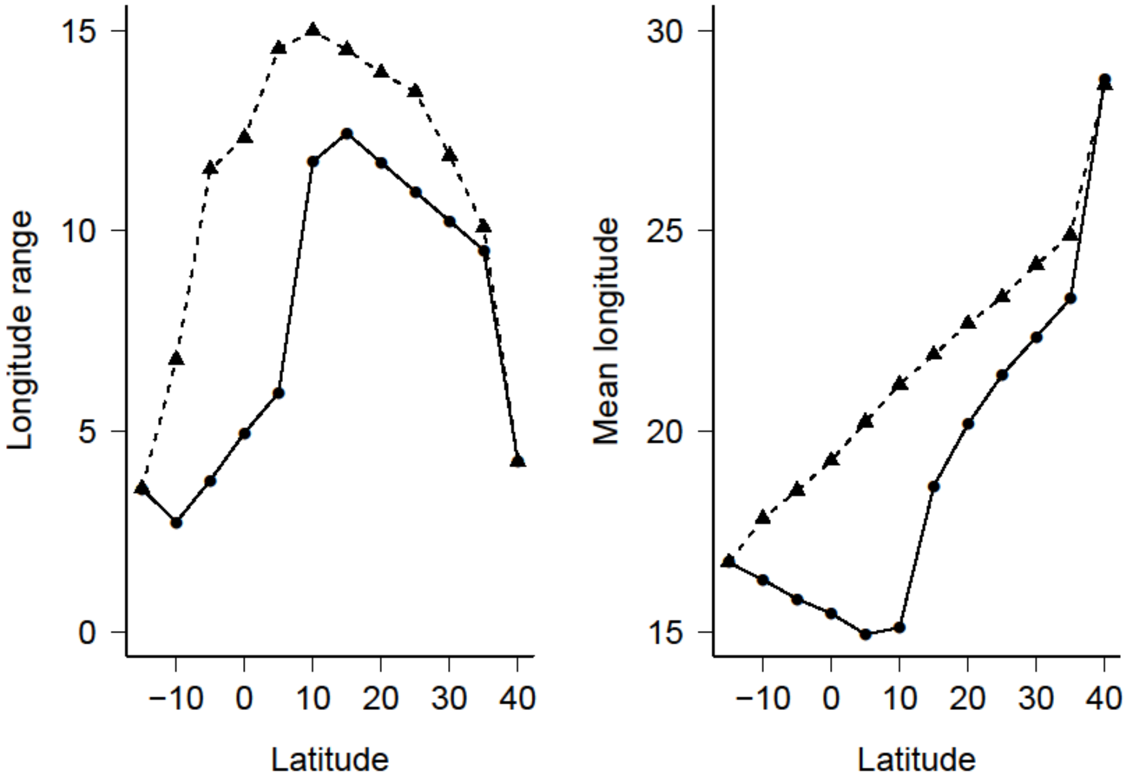

*Figure 3.6. Standard deviation and mean of simulated random autumn migration routes (dashed line), and the observed migration patterns of tracked Red-footed Falcons (solid line) at every 5° latitudes between 40°N and 15°S. The scatter and mean longitudes significantly deviated from random between 10°N–10°S, while they were coherent with the null distributions between 35°N–10°N.*

tances through the rainforest. Whereas the narrowest possible route through the forest is ca. 400 km (Olson et al., 2001), the estimated shortest routes of these falcons ranged from 672 to 915 km, suggesting that individuals may double their routes above the forest to avoid rain.

The behaviour of these birds raises the question of whether the area of convergence possessed particular precipitation patterns. We found that both parameters had a marked spatial pattern (Fig. 3.8 A and B) characterized by lower volume and variability of precipitation. To estimate rainfall risk from the migrants' perspective we created a risk index as the product of median daily precipitation and MAD scaled to a 0-10 interval. This index is low when daily precipitation and its variability is low, and high when rainfall or its unpredictability is high. The mean risk index was significantly (ANOVA, F1,558=80.69, p<<0.001) lower by 58% in the area delineated by the eastern and westernmost routes of the Red-footed Falcons (mean=2.4 ± 1.2 SD) versus the rest of the rainforest (mean 4.7 ± 1.84 SD). Moreover, the spatial pattern of the risk index comprised a 200 to 250 km corridor extending south of the rainforest (Fig. 3.9 A).

The finding that Red-footed Falcons migrate through a corridor of lower rainfall risk suggests that Hobbies had navigated a similar route also to minimize the risk of encountering heavy rain. Although, the precise location points of each Hobby were not reported, the published trajectories are sufficient to evaluate whether Hobbies and Red-footed Falcons pursued similar strategies. The mean routes of the five Hobbies (1 from Germany, 4 from Sweden) tracked between 2005–2010 passed through the low risk corridor used by Red-footed Falcons (Fig. 3.10). Moreover, the mean routes of Hobbies, and the individual trajectories of Red-footed Falcons, continued to coincide with lower risk zones for hundreds of kilometers beyond the southern extent of the rainforest (Fig. 3.10 A and B).

We also examined the published accounts of the migration routes of the only other falcon species to have been satellite-tracked crossing the African rainforest. Eleonora's Falcons, which breed across the approx. 3500km expanse of the Mediterranean and winter in Madagascar, are likely to face diverse trade-offs when crossing the equatorial region according to their starting point. The advantage of circumventing the rainforest may be higher for individuals from more westerly origins during their autumn migration. Naive raptors are considered to lack the experience to overcome adverse meteorological conditions that may deter them from pursuing their intended course (Thorup et al., 2003). Therefore, to be consistent with our study of adult Red-footed Falcons, and our examination of adult Hobbies, we evaluated only adults in the Eleonora's Falcon studies, which were reported by three research teams tracking 15 adults between 2003–2010 (Gschweng et al., 2008; Kassara et al., 2012; López-López et al., 2010). Six of the tracked 13 individuals entered the rainforest whereas the other birds circumnavigated the area (Fig. 3.10 B). By overlaying the mean routes of both groups with the rain risk map we discovered another east-west low risk corridor used by individuals entering the rainforest in North-east Congo. The later individuals covered ca. 1200 km over continuous woodland and apparently passed through a pronounced east-west lower risk corridor (Fig. 3.10 B). Moreover, the routes of these birds show similar route convergence near the exit of the corridor, as did Hobbies and Red-footed Falcons near the western corridor (Fig. 3.10 B).

Our findings demonstrate that the risk of encountering rain in the specific period migrants are likely to cross the African tropical system in autumn has a marked spatial pattern forming lower risk corridors. Individuals of multiple species spanning nearly a decade long tracking effort apparently converged to these corridors. Heavy rain has been associated with mass mortality of avian migrants (Newton, 2007) as drenched plumage reduces flight capabilities. Therefore precipitation in tropical regions may be hazardous to migrants on its own and may act as an integrative factor that affects

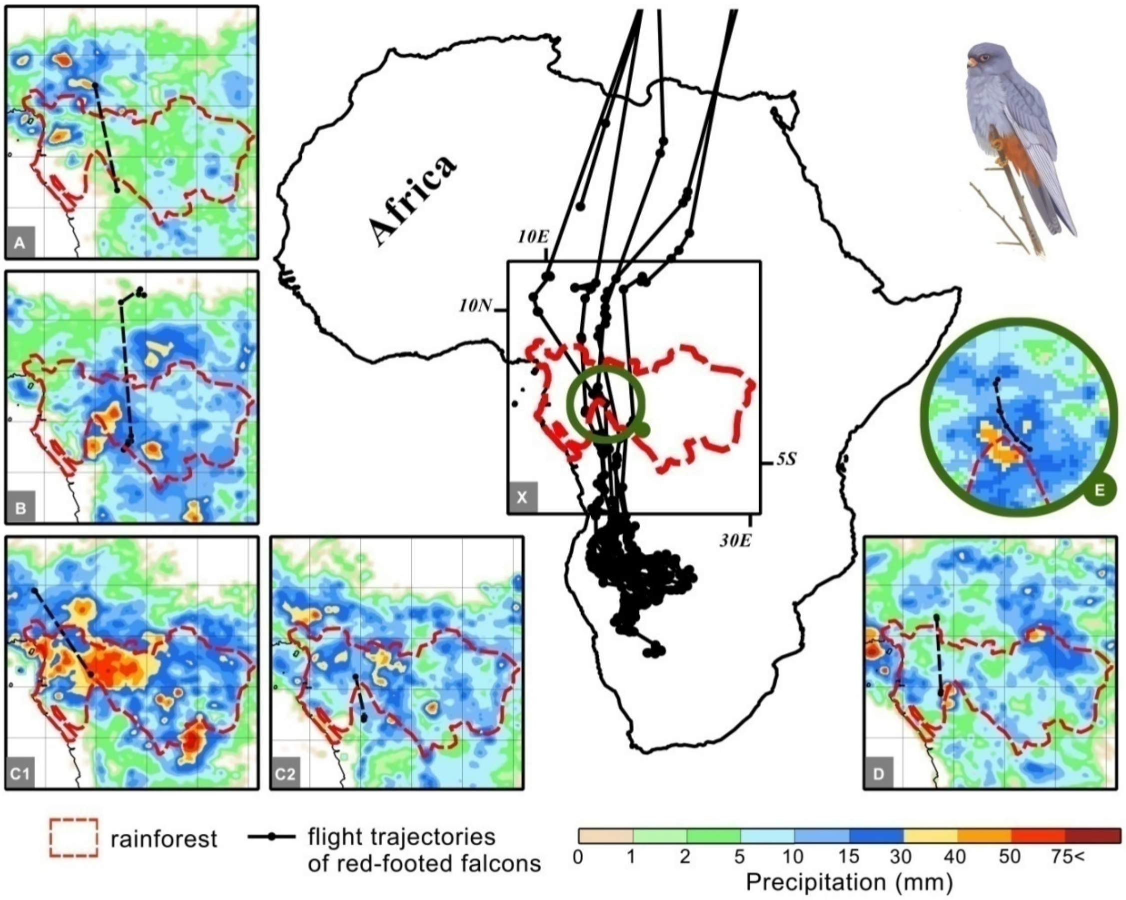

*Figure 3.7. Autumn migration routes of satellite-tracked Red-footed Falcons through Africa, and the immediate precipitation distribution at the time of individual rainforest crossing. The extent of the rainforest biome derived from Mayaux et al. (2004). The rainfall estimates were calculated using the date of coordinates at the starting point (i.e. north of the rainforests) and the date at end of the segment represented, thus corresponding to the interpolated routes (black dashed lines). Since the location of the birds was known every ca. 48 hours, we used the three day maximum value starting from the last known coordinate north of the rainforest. A) shows the first of the birds to cross in relatively low precipitation. B) shows the second individual to cross. The bird's trajectory indicates that it avoided the two major rain centres present in the area and presumably flew in between them amidst moderately heavy rain. C1) and C2) correspond to the same individual albeit in two consecutive triads. This bird headed south-west from northern Nigeria and flew in to a major storm system ranging across the whole western rainforest zone. It halted southward movement for 3-4 consecutive days and only commenced migration amidst lower rainfall intensity. D) shows the fourth individual to cross the rainforest in moderate rainfall. This individual also circumvented a rain center from the west just short of exiting the rainforest. E) shows the fifth individual, whose transmission cycle was obtained while flying above the rainforest between 13:40 and 21:40 CET on Oct. 6 2009, therefore we depicted the daily rainfall pattern. This bird altered its flight path to avoid flying through heavy rain, keeping a distance of ca. 20 kms from the edge of the intense precipitation*

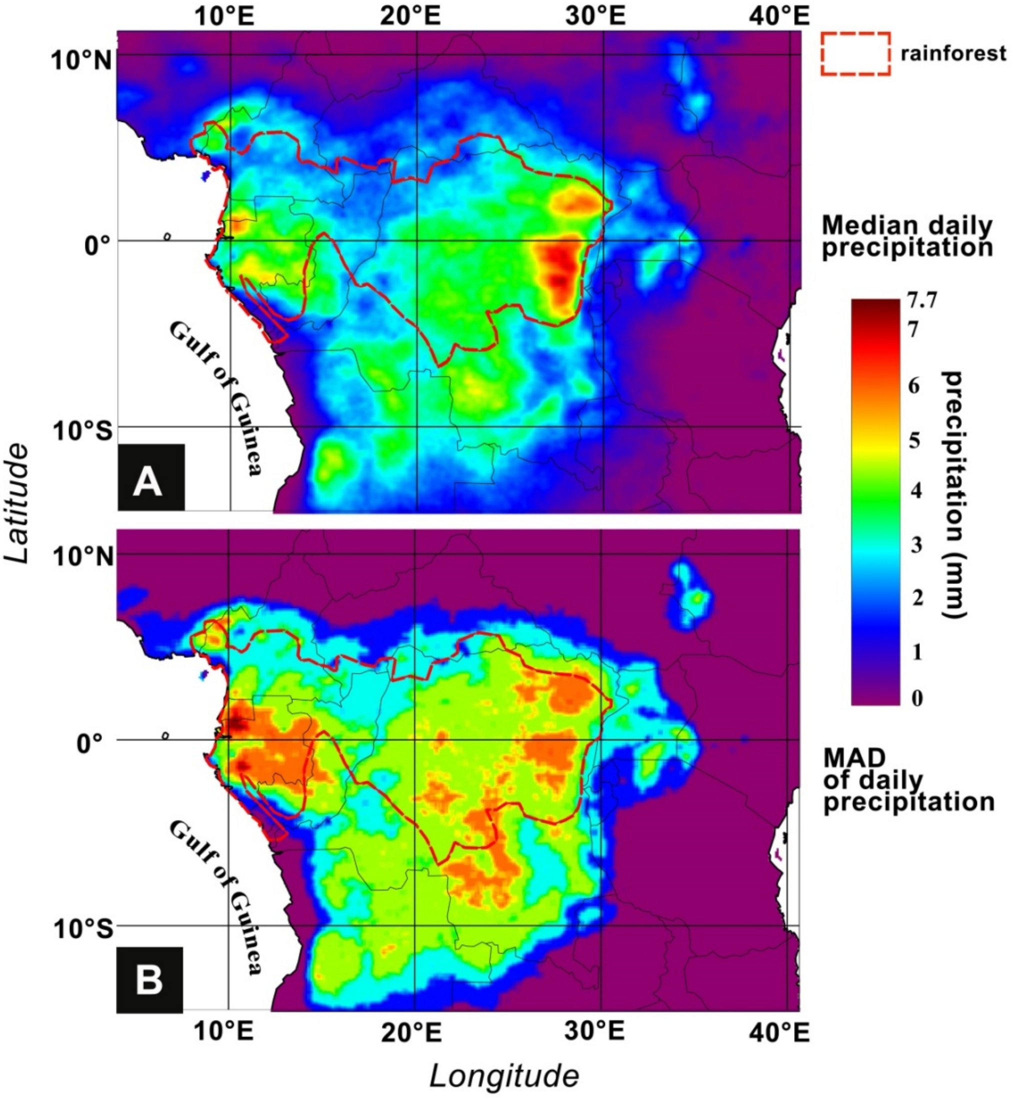

*Figure 3.8. Median (A) daily precipitation and MAD rates (B) of October and November between 2001–2011 in the Congo Basin.*

predation avoidance, foraging efficiency and other possible parameters that further increase the costs of traversing predictably high rainfall areas. Migrants may have evolved to overall avoid such high risk areas, or as our study demonstrates aim to cross at lower risk zones. Our results raise the additional question of how birds locate lower risk corridors.

One possibility is that migrants, through experience or instinct, cue on the edges of the rainforest or on other stable geographic features that correspond with precipitation patterns. Cuing may also entail copying more experienced individuals (Chernetsov et al., 2004; Danchin et al., 2004), or using innate navigational mechanisms (Alerstam, 2006; Chernetsov et al., 2008; Holland et al., 2009).

The use by migrants of lower risk corridors through the African rainforest leads to the prediction that if such corridors exist in other rainforests, migrants should exploit them, suggesting that we should find this in the shape of the migration pattern of other tropical regions. Many evidence indicate that climate change impacts the fitness of migratory birds in various ways (Jonzén et al., 2006). Further studies of lower precipitation corridors should be explored in the context of climate change given its potential to alter the survival of migrants cuing on adaptive migration routes that may be subject to change.

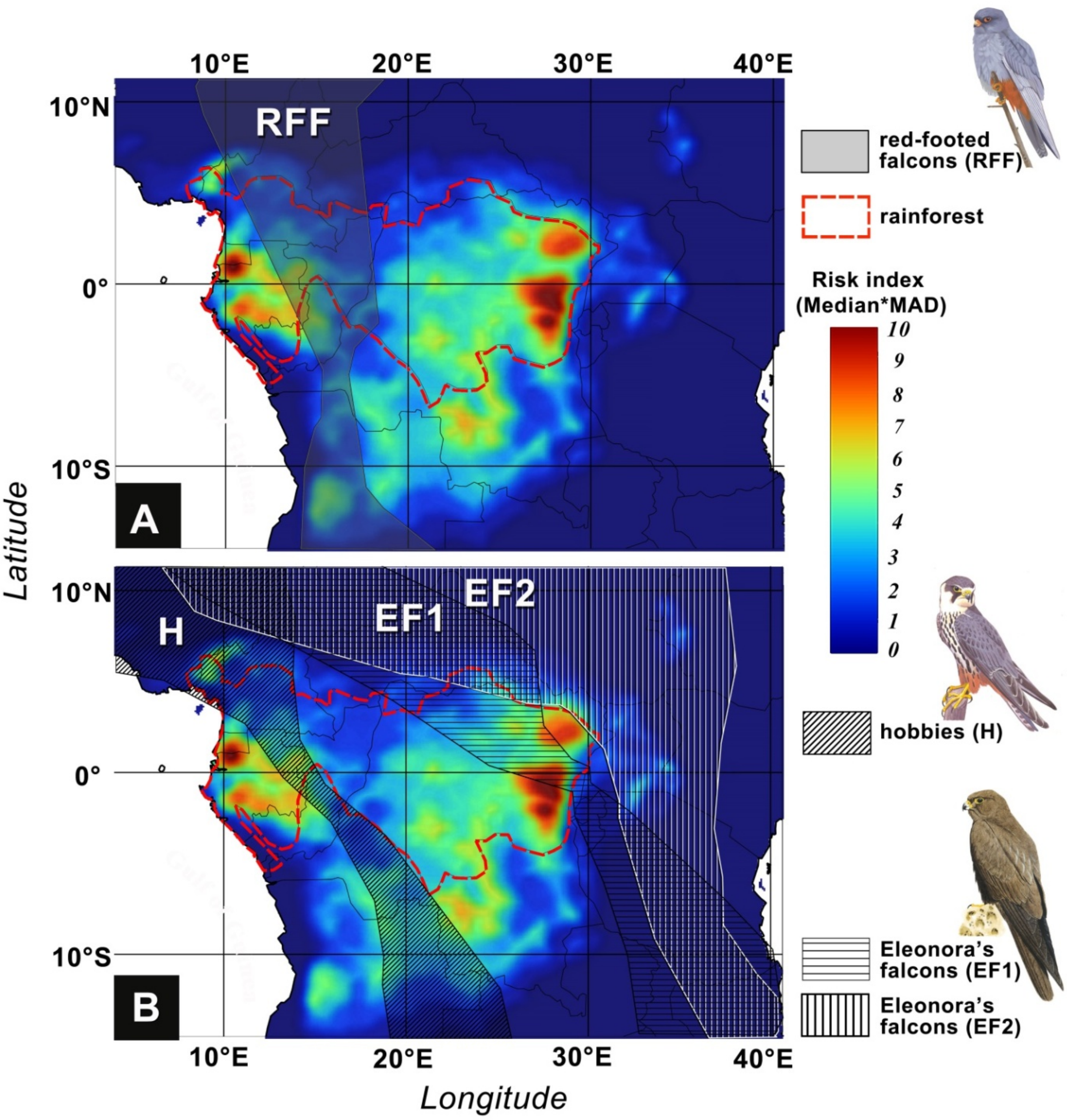

*Figure 3.9. Converging routes of Red-footed Falcons, Hobbies and Eleonora's Falcons. Figures were drawn by connecting the eastern and westernmost location points of tracked individuals. Individuals of all three species show route convergence in the Congo Basin. A) depicts the funneling of tracked Red-footed Falcons in 2009. These birds migrated in a relatively wide area within the rainforest, as a consequence of the avoidance tactics depicted in Fig. 3.6 B) shows the combined routes of 5 Hobbies and 13 Eleonora's Falcons. Individuals of the latter species that did enter the rainforest show a similar route convergence to that of the previous two species in between two high precipitation risk peaks*

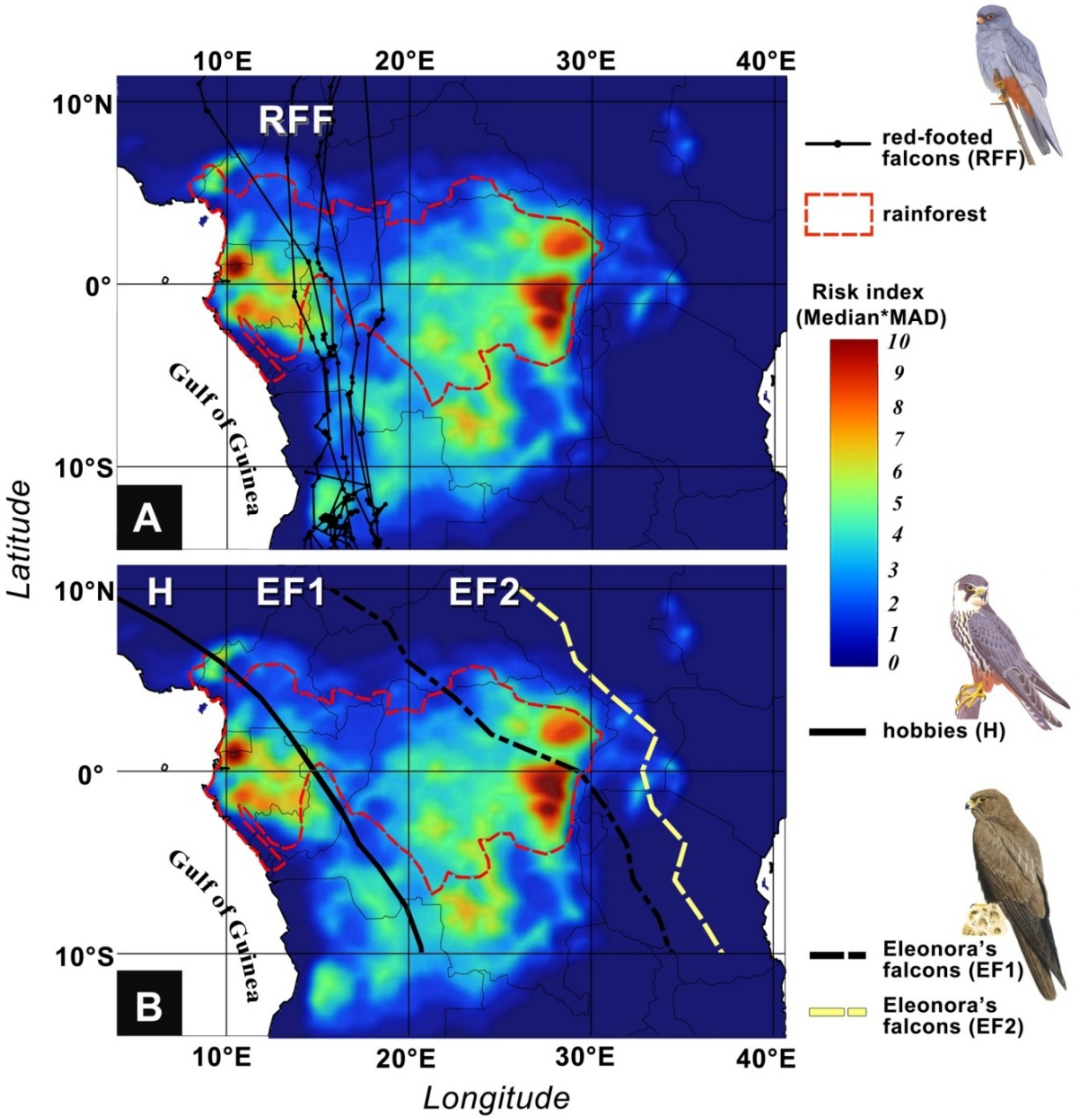

*Figure 3.10. The mean routes of tracked trans-equatorial migrant falcon species through the African tropics in relation to the spatial distribution of precipitation risk. The latter is defined as median * median absolute distance (MAD) of estimated daily precipitation of October and November (2001–2011), rescaled to a range of 0–10. A) shows the flight trajectories of 5 satellite tracked Red-footed Falcons (RFF). B) shows the approximate mean routes of Hobbies, (H), and Eleonora's Falcons, (EF1 and EF2). We differentiated Eleonora's Falcon individuals that entered the rainforest (EF1) from those who circumnavigated it (EF2) and calculated mean latitudes for every second longitude between 10N and 10S. Red-footed Falcons and Hobbies crossed the Congo Basin through a well defined north-south corridor of lower precipitation risk. The approximate mean route Eleonora's Falcons that entered the rainforest apparently crosses in between two major high precipitation risk areas at the eastern extreme of the rainforest*

# Summary of main scientific results

Here I briefly list the main results of my thesis:

1. I show that Red-footed Falcon breeding colony selection can be modelled effectively with landscape scale habitat variables, they prefer breeding sites where within the potential home-range grasslands have high, while urban areas, forests and open water surfaces have low percentages.
2. I identified a possible cause of reported breeding range shrinkage of Red-footed Falcons; Rooks, their nest-host species, have possibly altered their breeding site selection to urban areas in regions where the falcons have become extinct.
3. I show that species distribution modelling using landscape scale habitat variables, machine learning algorithms and their ensemble predictions are capable of identifying conservation target areas for Red-footed Falcons in areas where nature conservation resources are lacking.
4. I analysed the pre-migratory individual trajectories of satellite tracked Red-footed Falcons and the results indicate that tracked individuals show plastic behaviour on a continental scale when selecting pre-migratory roost sites.
5. I identified two and five yet unknown potential pre-migratory Red-footed Falcon roost sites in Hungary and in the Ukraine, respectively.
6. I present correlative evidence that migrant Red-footed Falcons traversing the African Congo Basin optimize their routes to avoid precipitation.
7. I demonstrate the existence of low rainfall risk corridors in the Congo Basin which Red-footed Falcons and tracked individuals of two sister species utilize when traversing the region.
8. For the first time I present correlative evidence that the African rainforest is potentially a meteorological barrier for avian migrants.

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