

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

PÉTER FEHÉRVÁRI^{1*}, BENCE LÁZÁR², PÉTER PALATITZ³, SZABOLCS SOLT³,
ATTILA NAGY⁴, MÁTYÁS PROMMER³, KÁROLY NAGY³ & ANDREA HARNOS²



Péter Fehérvári, Bence Lázár, Péter Palatitz, Szabolcs Solt, Attila Nagy, Mátyás Prommer, Károly Nagy & Andrea Harnos 2014. Pre-migration roost site use and timing of post-nuptial migration of Red-footed Falcons (*Falco vespertinus*) revealed by satellite tracking. – Ornis Hungarica 22(1): 36–47.

Abstract Red-footed Falcons are gregarious trans-equatorial migrants, forming up to several thousand strong 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 we investigate the autumn movements of 8 individuals caught and satellite-tagged within the Carpathian Basin. We found that birds may use multiple roost sites that can be separated by large distances. A single individual's home range was 88 km² (80% kernel home range) and was near concentric to the roost site. Two individuals travelled to southern Ukraine soon after tag-deployment. Our 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. 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, we cross-referenced the departure dates of tagged individuals with the 6 year means of counted individuals. The tagged birds initiated migration with the first 25% percent of the surveyed population.

Keywords: *Falco vespertinus*, post-nuptial migration, Platform Terminal Transmitter, gregarious behaviour, home range extent

Összefoglalás A transzekvatoriális vonuló kék vércsék a fészkelési időszak után, a vonulást megelőző időszakban csoportos éjszakai, úgynevezett gyülekezőhelyet alakítanak ki. Ez a periódus feltehetően igen fontos a hosszú távú vonulók túlélése szempontjából. Ebben az időszakban a Kárpát-medence különböző területein 8, műholdas nyomkövetővel felszerelt madár őszi mozgásmintázatát vizsgáltuk. Eredményeink szerint a madarak akár több, egymástól nagy távolságra lévő gyülekezőhelyet is használhatnak. Az egyik egyed mozgáskörzete 88 km² volt (80% Kernel home range becslés), és közel koncentrikusan helyezkedett el a gyülekezőhelyhez viszonyítva. Két egyed Dél-Ukrajnába repült nem sokkal a jeladó felhelyezése után. Eredményeink azt mutatják, hogy még a kisszámú, műholdas jeladóval felszerelt madár viselkedése is nagyban különbözött. Az éjszakai adatok alapján 2 magyarországi, valamint 6 dél-ukrajnai lehetséges új gyülekezőhelyet határoltunk be. A Kárpát-medencében 2006 és 2011 között hetenként végzett nemzetközi felmérés adatait felhasználva összevetettük a jelölt madarak indulási adatait a populáció 6 éves átlagaival. A jelölt madarak a felmért populáció első 25%-ával együtt kezdték a vonulást.

Kulcsszavak: *Falco vespertinus*, őszi vonulás, műholdas jeladó, pre-migráció, mozgáskörzet, gyülekezőhely

¹ Department of Zoology, Hungarian Natural History Museum, 1088 Budapest, Baross utca 13., Hungary, e-mail: fpeter17@gmail.com

² Department of Biomathematics and Informatics, Faculty of Veterinary Sciences, Szent István University, 1078 Budapest, István utca 2., Hungary

³ Red-footed Falcon Conservation Working Group, MME/BirdLife Hungary, 1121 Budapest, Költő utca 21., Hungary

⁴ Milvus Group, Bird and Nature Conservation Association, 540343, Crinului St. 22, Tîrgu Mures, Romania

*corresponding author

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 1990). Despite its presumable influence on survival, the pre-migration period – i.e. the period after breeding and before the commencement of autumn migration (Rivera *et al.* 1998, 1999, Pagen *et al.* 2000) – 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 & Furness 1984) is not uncommon, and several species may also form common large roost sites (Newton 1998, Kruckenberg & Borbach-Jaene 2004, de Frutos *et al.* 2007, Lambertucci *et al.* 2008, Catry *et al.* 2010). Intriguingly, only a handful of raptors breeding in the Western Palaearctic are known to form pre-migratory and wintering roost sites (Ferguson-Lees & 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 (Horváth 1956, Fehérvári *et al.* 2009, Fehérvári *et al.* 2012), their autumn roosting behaviour has only recently been described in detail (Borbáth & 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 (Fehérvári *et al.* in prep).

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 (Fehérvári *et al.* in prep), 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.

Materials and Methods

Platform Terminal Transmitter

We mist-netted 8 adult female-above average weighed Red-footed Falcons and fitted them with 5 g 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, Gschweng *et al.* 2008). At the time of harnessing, the 5 g 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 approxi-

mately 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 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 be-

tween 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 sites, therefore we visually estimated the potential extent of an error buffer of 5 km around the fitted MCPs. This error buffer seems to be relatively large, however the location of roost sites may slightly vary between years (Borbáth & 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 pin-point 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 consi-

ID	Number of roost sites used	Number 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

* Tagged Red-footed Falcons spending the pre-migration period in southern Ukraine.

Table 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

1. táblázat A nyomkövetett madarak (n=5) által használt gyülekezők száma, a gyülekezőhely váltások száma és a szélességi és hosszúsági eltérés terjedelme a pre-migrációs időszakban kapott lokalizációs pontok alapján. Az első két paramétert az éjszakai pontok alapján (este 9 és reggel 6 óra között helyi idő szerint) kaptuk. Az Ukrajnában tartózkodó madarak többször váltottak gyülekező helyet, illetve nagyobb területet jártak be Kárpát-medencében maradó társaikhoz képest

dered the location points obtained during the day. In case an individual had a valid location point after 15 p.m. over ~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 2011) and R 2.13.1 (Calenge 2006, R Development Core Team 2011).

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 1*). The 80% kernel home range estimate of a single individual (indiv. A) was 88 km² and was near concentric around the roost site (*Figure 1*).

Two tagged birds (indiv. D, indiv. E, see *Table 1* and *Figure 2*) left the Carpathian Basin and moved to southern Ukraine within days after PTT deployment, staying in the region until the onset of migration. The dis-

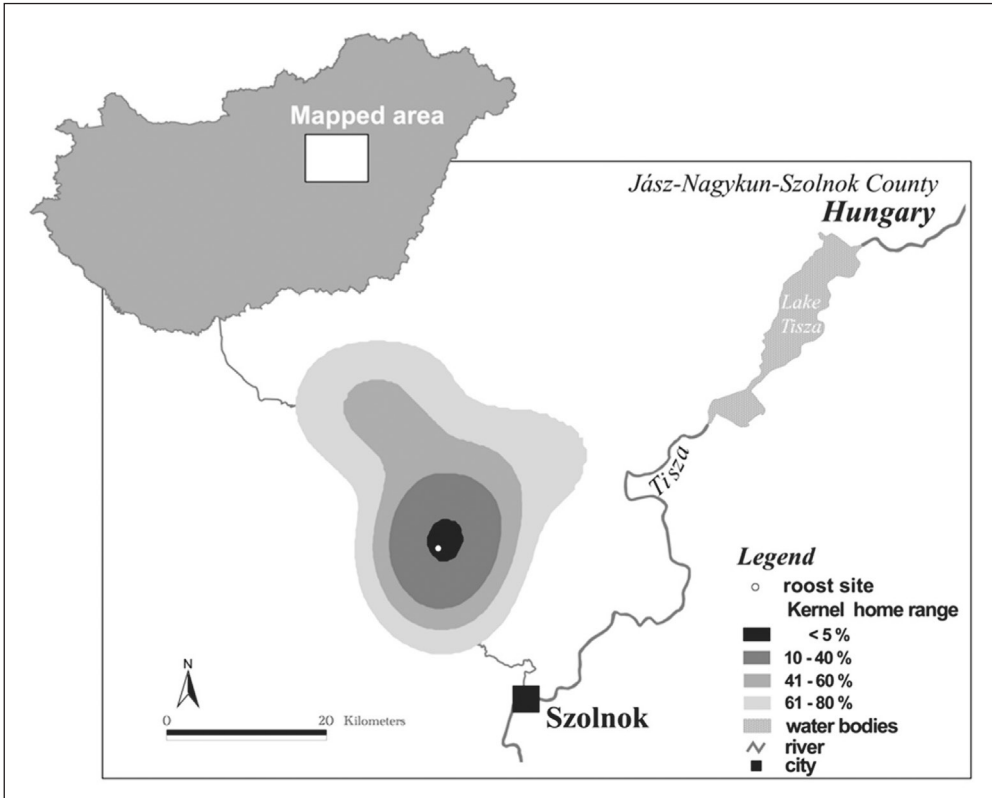


Figure 1. Kernel home-range estimate of pre-migration foraging area extent of a single individual (individ. A) based on satellite localization points during the day. The 80% Kernel home-range (88 km²) is highlighted and reported to allow conservative estimate of a foraging area extent and to exclude localization points deriving from days when the individual utilized a neighbouring roost site. The home-range is near concentric, centring the roost site

1. ábra Nappali lokalizációs pontok alapján számított kernel home range becslés az A egyed esetében. A 80% kernel becslést használtuk, amely meglehetősen konzervatív, azonban ezzel elkerülhető azon pontok bevétele a becslésbe, amikor a madár egy szomszédos gyülekezőn aludt. A mérések alapján a madár mintegy 88 km²-es területet használt vadászterületként, ami szinte koncentrikusan helyezkedik el a gyülekezőhelyez képest

tance from the original trapping site to the first known roost site was 582 km, and 657 km for indiv. D and indiv. E, respectively. These two birds seemed to have changed roost sites more often, than those staying within the Carpathian Basin, and they have also moved in a larger area (Table 1). Only one of the seven known roosting sites in the Ukraine was used by these birds, however we were able to identify 5 new poten-

tial roost sites (Table 2, Figure 2). We were also able to locate two new potential roost sites in Hungary (Table 2).

The timing of autumn migration of all tagged birds fell between the 37th and 38th week of the year (Figure 3). 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

Country	Region/County	Latitude	Longitude
Hungary	Bács-Kiskun	19.927	46.724
Hungary	Hajdú-Bihar	21.128	47.392
Ukraine	Tatarbunarskyi	29.986	45.815
Ukraine	Ovidiopol'skyi	30.484	46.160
Ukraine	Bereziv'skyi	30.883	47.415
Ukraine	Novoodszkyi	32.013	47.258
Ukraine	Berislaw'skyi	33.178	46.848

Table 1. Coordinates of buffer polygon centroids of new potential Red-footed Falcon pre-migration roost sites in Hungary and in the Ukraine

1. táblázat Az éjszakai lokalizációs pontok köré húzott pufferzónák súlyponti koordinátái. Ezek közelében feltehetően eddig ismeretlen gyülekezőhelyek vannak

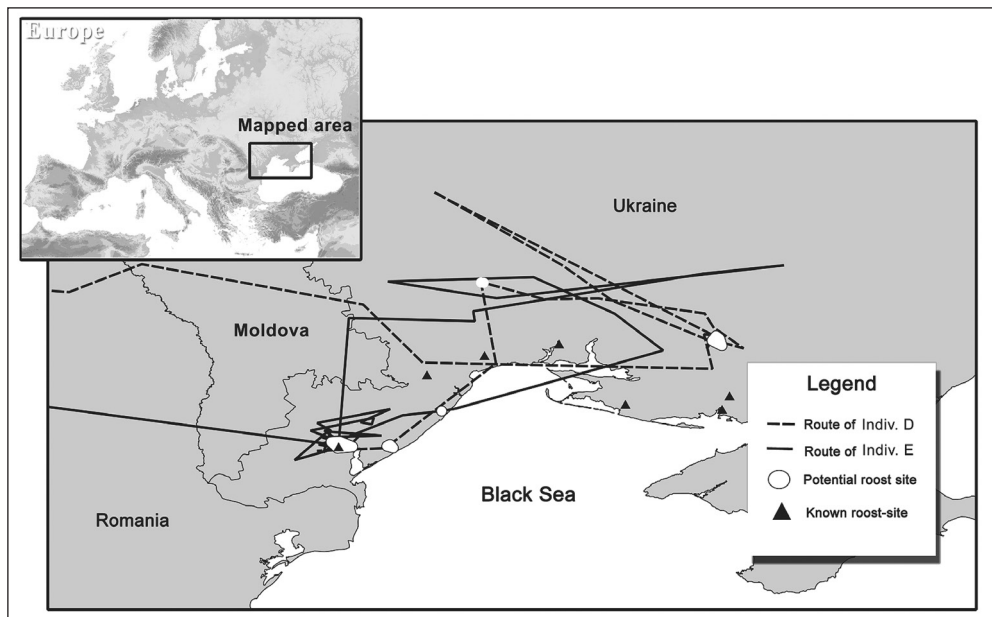


Figure 2. Movement patterns and roost site usage of two tagged Red-footed Falcons spending the pre-migration period in the southern Ukraine. These two individuals seemed to be more prone to change roost sites compared to the individuals remaining in the Carpathian Basin, and also moved in a larger area. Their localization points also helped identify 5 new potential roost sites in the Ukraine

2. ábra A pre-migrációs időszakban Ukrajnában tartózkodó madarak mozgásmintázata. Ez a két egyed többször váltott gyülekezőhelyet, és nagyobb területen is mozgott. A tőlük származó pontok alapján 5 új gyülekezőhelyet sikerült azonosítani

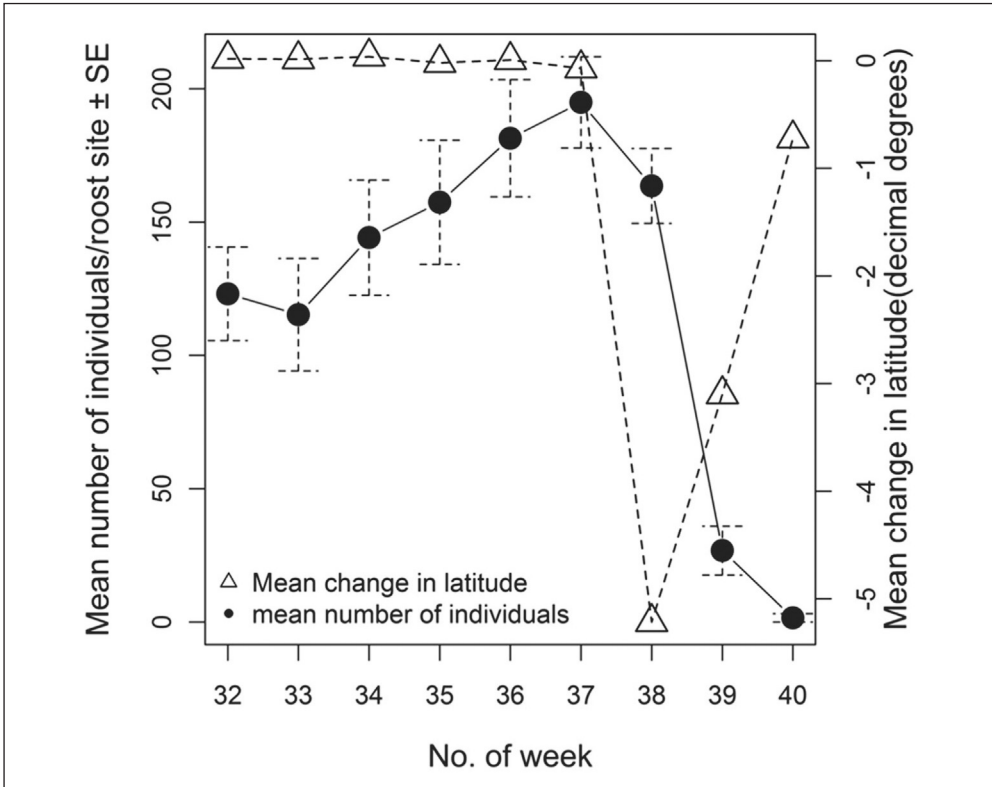


Figure 3. Departure timing of satellite tagged Red-footed Falcons and temporal dynamics of the number of roost site using Red-footed Falcons. The first vertical axis refers to the mean number of individuals at the roost sites within the Carpathian Basin (2006–2011). The second vertical axis scales the 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

3. ábra A jelölt kék vércsék vonulási időzítése és a szinkronszámlálások alapján becsült indulási idő. Az első függőleges tengelyen a szinkron számlálások alatt becsült madarak átlagai szerepelnek 2006 és 2011 között. A második függőleges tengelyen a relatív szélességi elmozdulás mértéke (két egymást követő pont közötti észak-déli távolság) látható. A jelölt madarak a korai indulókkal együtt kezdték meg vonulásukat a 37. és a 38. héten. Összességében a gyülekezők gyorsan ürülnek ki, a populáció vonulási időzítése meglepően konzervatív

38th and the 39th week, however a smaller proportion of the population is presumed to leave the pre-migration period a week earlier (Figure 3). Roughly, the tagged birds departed together with the earliest individuals in the 38th week of the year.

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 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 (Haraszthy & Palatitz 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 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 straightforward 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 (*Falco naumanni*) are close relatives of Red-footed Falcons and have similar life history traits (Cramp & 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, Tella *et al.* 1998, Franco *et al.* 2004). 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 well 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 ne-

cessity 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 (Danchin *et al.* 2004, Ahlering *et al.* 2010) 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 & Christie 2001) may utilize soaring, flapping flight (Shirihai *et al.* 2000) and may also migrate at night (Fehérvári *et al.*, 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.

Acknowledgements

This study was prepared within the scope of the LIFE Nature project titled 'Conservation of *F. vespertinus* in the Pannonian Region' (LIFE05 NAT/H/000122). We are thank Dr. Tibor Csörgő and two anonymous reviewers for their valuable comments on earlier versions of this manuscript. Monitoring data was collected by the members of MME/BirdLife Hungary's Red-footed Falcon Working Group, Bükk National Park Directorate, Hortobágy National Park Directorate, Körös-Maros National Park Directorate, Duna-Ipoly National Park Directorate, and various other volunteers, for whom we are grateful. This work was supported by the Research Faculty Grant 2014 of the Szent István University, Faculty of Veterinary Science.

References

- Ahlering, M. A., Arlt, D., Betts, M. G., Fletcher, Jr., R. J., Nocera, J. J. & Ward, M. P. 2010. Research needs and recommendations for the use of conspecific-attraction methods in the conservation of migratory songbirds. – *The Condor* 112: 252–264. DOI: 10.1525/cond.2010.090239
- Alerstam, T. 1990. *Bird Migration*. – Cambridge University Press, Cambridge, pp. 420
- Berthold, P. 1996. *Control of bird migration*. – Chapman & Hall, London, pp. 355
- BirdLife International 2007. Conservationists appalled at Red-footed Falcon massacre. http://www.birdlife.org/news/news/2007/10/cyprus_falcon_massacre.html. Accessed: 01.11.2012.
- Borbáth, P. & Zalai, T. 2005. Kék vércsék (*Falco vespertinus*) őszi gyülekezése a Hevesi-síkon [Autumn roost site of Red-footed Falcons in the Heves Plains]. – *Aquila* 112: 39–44. (in Hungarian with English Summary)
- Caccamise, D. F., Lyon, L. A. & Fischl, J. 1983. Seasonal patterns in roosting flocks of starlings and Common Grackles. – *The Condor* 85: 474–481.
- Calenge, C. 2006. The package ‘adehabitat’ for the R software: a tool for the analysis of space and habitat use by animals. – *Ecological Modelling* 197: 516–519. DOI: 10.1016/j.ecolmodel.2006.03.017
- Catry, I., Dias, M. P., Catry, T., Afanasyev, V., Fox, J., Franco, A. & Sutherland, W. J. 2011. Individual variation in migratory movements and winter behaviour of Iberian Lesser Kestrels *Falco naumanni* revealed by geolocators. – *Ibis* 153(1): 154–164. DOI: 10.1111/j.1474-919X.2010.01073.x
- Cramp, S. & Simmons, K. E. 1980. *The Birds of the Western Palearctic*, Vol. 2. – Oxford University Press, Oxford, New York, pp. 695
- Danchin, E., Giraldeau, L. A., Valone, T. J. & Wagner, R. H. 2004. Public information: from nosy neighbors to cultural evolution. – *Science* 305: 487–491. DOI: 10.1126/science.1098254
- de Frutos, A. 2008. Importance of the premigratory areas for the conservation of Lesser Kestrel: space use and habitat selection during the post-fledging period. – *Animal Conservation* 11: 224–233. DOI: 10.1111/j.1469-1795.2008.00173.x
- de Frutos, A., Olea, P. P. & Vera, R. 2007. Analyzing and modelling spatial distribution of summering Lesser Kestrel: The role of spatial autocorrelation. – *Ecological Modelling* 200: 33–44. DOI: 10.1016/j.ecolmodel.2006.07.007
- Donázar, J. A., Negro, J. J., Hiraldo, F. & Hiraldo, F. 1993. Foraging habitat selection, land-use changes and population decline in the Lesser Kestrel *Falco naumanni*. – *Journal of Applied Ecology* 30: 515–522.
- Eiserer, L. A. 1984. Communal roosting in birds. – *Bird Behaviour* 2: 61–80.
- Fehérvári, P., Solt, Sz., Palatitz, P., Barna, K., Ágoston, A., Gergely, J., Nagy, A., Nagy, K. & Harnos, A. 2012. Allocating active conservation measures using species distribution models: a case study of Red-footed Falcon breeding site management in the Carpathian Basin. – *Animal Conservation* 15(6): 648–657. DOI: 10.1111/j.1469-1795.2012.00559.x
- Fehérvári, P., Harnos, A., Neidert, D., Solt, Sz. & Palatitz, P. 2009. Modeling habitat selection of the Red-footed Falcon (*Falco vespertinus*): A possible explanation of recent changes in breeding range within Hungary. – *Applied Ecology and Environment* 7: 59–69.
- Fehérvári, P., Neidert, D., Solt, Sz., Kotymán, L., Szövényi, G., Soltész, Z. & Palatitz, P. 2007. Kék vércse élőhelypreferencia vizsgálata – egy tesztév eredményei [Red-footed Falcon Habitat Preference Analysis – results of a test year]. – *Heliaca* 3: 51–59. (in Hungarian with English Summary)
- Ferguson-Lees, J. & Christie, D. A. 2001. *Raptors of the World*. – Houghton Mifflin Company, Boston, USA, pp. 992
- Forsman, D. 1999. *The raptors of Europe and the Middle East: a handbook of field identification*. – T & AD Poyser, London
- Franco, A. M. A., Catry, I., Sutherland, W. J. & Palmeirim, J. M. 2004. Do different habitat preference survey methods produce the same conservation recommendations for Lesser Kestrels? – *Animal Conservation* 7: 291–300. DOI: 10.1017/S1367943004001465
- Gschweng, M., Kalko, E. K. V., Querner, U., Fiedler, W. & Berthold, P. 2008. All across Africa: highly individual migration routes of Eleonora’s Falcon. – *Proceedings of the Royal Society, Series B*: 275: 2887–2896. DOI: 10.1098/rspb.2008.0575
- Haraszthy, L. & Palatitz, P. 2009. Kék vércse [Red-footed Falcon]. – In: Csörgő, T., Karcza, Zs., Halmos, G., Magyar, G., Gyurácz, J., Szép, T., Bankovics, A., Schmidt, A. & Schmidt, E. (eds.) 2009. *Magyar madárvonulási atlasz [Hungarian Atlas of Bird Migration]*. – Kossuth Kiadó, Budapest, pp. 242–243. (in Hungarian with English Summary)
- Horváth, L. 1956. The life of the Red-legged Falcon (*Falco vespertinus*) in the Ohat Forest. – *Acta XI. Congressus Internationalis Ornithologici, Basel 1954*: 583–584.
- Kenward, R. 2001. *A manual for wildlife radio tagging*. – 2nd Edition, Academic Press, London, pp. 350
- Kostenko, M. 2009. Inventory of the breeding population of Red-footed Falcons in Ukraine: Spring-Sum-

- mer 2009. Project Report, Ukrainian Society for the Protection of Birds, Kiev (unpublished report, in English)
- Kruckenberger, H. & Borbach-Jaene, J. 2004. Do Greylag Geese (*Anser anser*) use traditional roosts? Site fidelity of colour-marked Nordic Greylag Geese during spring migration. – *Journal of Ornithology* 145: 117–122. DOI: 10.1007/s10336-004-0021-1
- Lambertucci, S. A., Luis Jácome, N. & Trejo, A. 2008. Use of communal roosts by Andean Condors in northwest Patagonia, Argentina. – *Journal of Field Ornithology* 79: 138–146. DOI: 10.1111/j.1557-9263.2008.00155.x
- López-López, P., Limiñana, R. & Urios, V. 2009. Autumn migration of Eleonora's Falcon *Falco eleonora* tracked by satellite telemetry. – *Zoological Studies* 48: 485–491.
- Metcalfe, N. B. & Furness, R. W. 1984. Changing priorities: the effect of pre-migratory fattening on the trade-off between foraging and vigilance. – *Behavioural Ecology and Sociobiology* 15: 203–206. DOI: 10.1007/BF00292976
- Mitchell, G. W., Taylor, P. D. & Warkentin, I. G. 2010. Assessing the function of broad-scale movements made by juvenile songbirds prior to migration. – *The Condor* 112: 644–654. DOI: 10.1525/cond.2010.090136
- Morton, M. L. 1992. Effects of sex and birth date on pre-migration biology, migration schedules, return rates and natal dispersal in the Mountain White-crowned Sparrow. – *The Condor* 94: 117–133.
- Newton, I. 1998. Population limitation in birds. – Academic Press, London, pp. 597
- Pagen, R. W., Thompson III, F. R. & Burhans, D. E. 2000. Breeding and post-breeding habitat use by forest migrant songbirds in the Missouri Ozarks. – *The Condor* 102: 738–747. DOI: 10.1650/0010-5422(2000)102[0738:BAPBHU]2.0.CO;2
- Palatitz, P., Fehérvári, P., Solt, S. & Boris, B. 2009. European Species Action Plan for the Red-footed Falcon *Falco vespertinus* Linnaeus, 1766. – European Commission
- Palatitz, P., Fehérvári, P., Solt, S., Kotymán, L., Neidert, D. & Harnos, A. 2011. Exploratory analyses of foraging habitat selection of the Red-footed Falcon (*Falco vespertinus*). – *Acta Zoologica Hungarica* 57: 255–268.
- Palatitz, P., Solt, S., Fehérvári, P., Ezer, Á. & Bánfi, P. 2010. Az MME Kékvércse-védelmi Munkacsoport 2008. évi beszámolója – A LIFE projekt (2006–2009) főbb eredményei [Annual report of MME/BirdLife Hungary's Red-footed Falcon Working Group – the major results of the project LIFE (2006–2009)]. – *Heliaca* 5: 12–17. (in Hungarian with English Summary)
- Quantum GIS Development Team, G. I. S. 2011. Quantum GIS Geographic Information System. – Open Source Geospatial Foundation Project. Source: <http://qgis.osgeo.org>.
- R Development Core Team. 2011. R: A Language and Environment for Statistical Computing. – R Foundation for Statistical Computing, Vienna, Austria. Source: <http://www.R-project.org>.
- Rivera, J. H., McShea, W. J., Rappole, J. H. & Haas, C. A. 1999. Postbreeding movements and habitat use of adult Wood Thrushes in northern Virginia. – *The Auk* 116(2): 458–466.
- Rivera, J. H., Rappole, J. H., McShea, W. J. & Haas, C. A. 1998. Wood Thrush postfledging movements and habitat use in northern Virginia. – *The Condor* 100: 69–78.
- Seaman, D. E., Millsapugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J. & Gitzen, R. A. 1999. Effects of sample size on kernel home range estimates. – *Journal of Wildlife Management* 63(2): 739–747.
- Shamoun-Baranes, J., Van Loon, E., Alon, D., Alpert, P., Yom-Tov, Y. & Leshem, Y. 2006. Is there a connection between weather at departure sites, onset of migration and timing of soaring-bird autumn migration in Israel? – *Global Ecology and Biogeography* 15: 541–552. DOI: 10.1111/j.1466-8238.2006.00261.x
- Shirihai, H., Yosef, R., Alon, D. & Kirwan, G. M. 2000. Raptor migration in Israel and the Middle East: a summary of 30 years of field research. – International Birding & Research Center in Eilat
- Steenhof, K., Bates, K. K., Fuller, M. R., Kochert, M. N., McKinley, J. O. & Lukacs, P. M. 2006. Effects of radiomarking on Prairie Falcons: attachment failures provide insights about survival. – *Wildlife Sociobiology* B 34: 116–126. DOI: 10.2193/0091-7648(2006)34[116:EOROPF]2.0.CO;2
- Strandberg, R., Klaassen, R. H. G., Hake, M., Olofsson, P. & Alerstam, T. 2009. Converging migration routes of Eurasian Hobbies *Falco subbuteo* crossing the African equatorial rain forest. – *Proceedings of the Royal Society, Series B*: 276: 727–733. DOI: 10.1098/rspb.2008.1202
- Tella, J. L., Forero, M. G., Hiraldo, F. & Donazar, J. A. 1998. Conflicts between Lesser Kestrel conservation and European agricultural policies as identified by habitat use analyses. – *Conservation Biology* 12: 593–604. DOI: 10.1111/j.1523-1739.1998.96288.x
- Weatherhead, P. J. 1983. Two principal strategies in avian communal roosts. – *American Naturalist* 121(2): 237–243.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. – *Ecology* 70: 164–168. DOI: 10.2307/1938423