

EXPLORATORY ANALYSES OF FORAGING HABITAT
SELECTION OF THE RED-FOOTED FALCON
(*FALCO VESPERTINUS*)

PALATITZ, P.¹, FEHÉRVÁRI, P.^{1,2}, SOLT, SZ.¹, KOTYMÁN, L.³, NEIDERT, D.⁴ and HARNOS, A.²

¹*MME/BirdLife Hungary, H-1121 Budapest, Költő u. 21, Hungary*

E-mail: palatitz.peter@mme.hu

²*Department of Biomathematics and Informatics, Faculty of Veterinarian Sciences
Szent István University, H-1071 Budapest István u. 2, Hungary*

³*Hungarian Academy of Sciences, Plant Protection Institute, Department of Zoology
H-1022 Budapest, Herman Ottó u. 15, Hungary*

⁴*Körös–Maros National Park, H-5040 Szarvas, Anna liget, Hungary*

The foraging habitat selection of Red-footed Falcons (*Falco vespertinus*) was investigated in a characteristic Hungarian habitat between 2006–2008. Potentially available habitat types were assessed within a 10 km² study site with remote sensing technologies. Altogether 18 adult birds were equipped with tail-mount VHF radio-tags and individually followed until visual contact to record location and foraging behaviour. Foraging areas were assessed with 100% Minimum Convex Polygons (MCP), global Manly's selectivity measures were used to detect population level habitat preference, and the eigenanalysis of selection ratios was carried out to partition the variability in individual habitat preference. We found large individual variability in the extent of foraging areas. Females had significantly smaller foraging areas compared to males, while males at the largest colony had significantly larger foraging areas compared to males of the smaller colonies. Global Manly's selectivity measures showed that birds significantly avoided intertilled crops, water surface, woods and artificial surfaces. The eigenanalysis of selection ratios partitioned individual habitat selection rates into two distinct groups; the first using grasslands and alfalfa while the second group of birds preferring grasslands and cereals. Positive habitat preference towards arable habitat types, indicate that species specific conservation efforts of this declining raptor should also focus on agricultural land use practices.

Key words: Red-footed Falcon, radio-telemetry, foraging habitat selection, design III eigenanalysis, Manly's selectivity

INTRODUCTION

Understanding the environment utilization of organisms over space and time is one of the main focus of modern ecology. Many animals – even the most mobile species – restrict their movement to specific home ranges (BURT 1943, JETZ *et al.* 2004) especially in the reproduction period. The extent, the habitat composition and the utilization of this space may provide intriguing support to better understand distribution and abundance of organisms (GAUTESTAD & MYSTERUD 2005), infection spread (KENKRE *et al.* 2007), predator–prey dynamics (LEWIS & MURRAY

1993), or habitat selection (RHODES *et al.* 2005). The latter proved to be eminently important in case of species with high nature conservation value, as these results help evaluate effective habitat management practices (SERGIO *et al.* 2003, FRANCO & SUTHERLAND 2004, MARTINEZ *et al.* 2007, ARROYO *et al.* 2009).

Recent developments in animal tracking methods (e.g. MATOSEVIC 2006), GIS and statistical tools (GUISAN & ZIMMERMANN 2000) are allowing to expand space use studies to a wide variety of species and facilitate well funded inferences on obtained results. The most common method used to assess how animals use space is deploying transmitters on the individuals, enabling researchers to sample individual movement patterns. The drawbacks of transmitter based tracking methods in avian species are that they are time-consuming, are often logistically difficult to carry out (e.g. PERROW *et al.* 2006), or are still very expensive (e.g. FRANCO *et al.* 2004). Moreover, the simple localizations of tracked individuals without the collection of additional variables (e.g. behavioural observations) are difficult to interpret. All of these disadvantages narrow to a common pitfall; a characteristic trait of these studies is that they often have low sample sizes, making population level inferences difficult.

The Red-footed Falcon (*Falco vespertinus*) is the sole facultative colonial raptor species of the Carpathian Basin, predominantly occupying rookeries for nesting (PURGER & TEPAVCEVIC 1999, PURGER 2001). This small falcon is in the focus of both national and international conservation efforts (strictly protected in Hungary, “near-threatened” in IUCN Red List, ANNEX I of EC Birds directive 79/409/EEC). Red-footed Falcons breed in steppe, pseudo-steppe, wooded steppe and extensive agricultural type habitats of Eurasia (DEL HOYO *et al.* 1992). The most frequent prey items of the species are invertebrates, mainly Orthoptera, Odonata, and Coleoptera, vertebrate prey items are mainly amphibians and small mammals (KEVE & SZIJJ 1957, CRAMP & SIMMONS 1977, HARASZTHY *et al.* 1994, PURGER 1998). A severe population decline was observed during the past 60 years (BAGYURA & PALATITZ 2004) coupled with a simultaneous contraction of breeding range within Hungary (FEHÉRVÁRI *et al.* 2009). A similar trend was recorded in adjacent Serbia (PURGER 2008). Habitat loss is one of the primary causes driving the decrease of avian diversity and species abundance (KREBS *et al.* 1999, MYERS *et al.* 2000, BUSTAMANTE 1997, LOPEZ-LOPEZ *et al.* 2007, CARRETE *et al.* 2002, DOLMAN & SUTHERLAND 1995). The recently completed European Species Action Plan for the Red-footed Falcon highlights that habitat loss and degradation is presumably a key element in the overall decline of this species, however there is a lack of basic knowledge obstructing the proper conservation management (PALATITZ *et al.* 2009).

To be in accordance with conservation needs the current paper is the first in series of studies conducted to reveal habitat selection and hunting efficiency of Red-footed Falcons.

The species is relatively easy to trap, observe and due to the colonial breeding they occur in high densities allowing to design and test innovative methods of space use study on moderate sample sizes. Our current objective with this study is to serve with basic information for conservation planning of the species, and to demonstrate that with optimally chosen tracking methodology and statistical tools, it is possible to reveal the variability of foraging area size and of resource selection present even when analysing a moderate sample size.

MATERIALS AND METHODS

Study site and habitat mapping

Field work was carried out between 2006–2008 at the Vásárhelyi-plains (46°28'16"N, 20°36'17"E), protected area of the Körös–Maros National Park Directorate (Fig. 1). This area of ca. 6000 ha together with its surroundings is one of the largest continuous grassland patches in southeastern Hungary and it holds one of the most characteristic alkali lakes of the region. Depending on the circumstances of the given year, altogether 60–120 pairs of Red-footed Falcons breed in 3 artificial nest-box colonies (C1, C2, C3 see Fig. 1), in addition to 5–15 solitary pairs. The three colonies showed large inter-annual variation in the number of breeding pairs (C1: 15–19 pairs, C2: 5–21 pairs C3: 9–48 pairs), however, C3 had the largest number of breeding pairs on average. A 10 × 10 km study area, centered around the oldest colony (C2), was designated prior to all field activity. Each year, a precise habitat map of the study area was prepared with the aid of remote sensing techniques. An Iconos-2 image was used to identify the habitat type of all habitat patches within the sample plot in 2006, while hyper-spectral aerial photographs were utilized to achieve the same at the end of 2007 and 2008. Habitat patches were defined either as the area of homogenous plant coverage (i.e. agricultural parcel) in the case of arable fields, or as the smallest area surrounded by line-type habitat attributes (e.g. dirt roads, canals) in the case of grasslands. We assigned an individual ID number and rendered habitat type attributes based on the reflected wavelength values of each pixel of the multispectral remote sensing images (for details see KRISTÓF *et al.* 2007). The habitat type categories were: grasslands, cereals, alfalfa, intertilled crops (e.g. maize and sunflower), artificial surface (e.g. roads, farm buildings), reedbeds, water surface and woods. The applied methodology did not allow the separation of fallow lands from grasslands, thus grasslands incorporate fallow type habitat patches in our study. Considerable inter-annual variation was observed in the relative extent of annual arable crops while the extent of natural habitats types remained constant.

Radio-telemetry

Altogether 10, 13 and 17 adult Red-footed Falcons breeding in the study site were trapped in 2006, 2007 and 2008, respectively. We used artificial and live decoys (eagle-owl; *Bubo bubo* and goshawk; *Accipiter gentilis*) placed in front of mist nets (BUB 1991) to catch adult falcons at the

breeding sites. Birds were colour-ringed and fitted with tail mount VHF radio transmitters (Biotrack TW-4, 3.5 gramms, www.biotrack.co.uk). The handling processes took ca. 15 minutes, and after release, the falcons were observed for the rest of the day to identify their nest and evaluate the possible effects of the tagging procedure. None of the marked birds showed signs of abnormal behaviour, usually as after a short preening period they returned to hunting or nest attendance.

In the first study year all birds were trapped at Colony 2 (Fig. 1 & Table 1), while in the following years birds of all three colonies and solitary breeders were tracked resulting in stratified sample of the population. In 2006, only 2 of the radio-tagged birds fledged their nestlings. The relatively low number of successfully breeding birds is presumably not the consequence of tagging procedure as a high nest failure rate was observed in the whole population in 2006 (FEHÉRVÁRI *et al.* 2008). Birds with failed breeding attempts left the study site to unknown locations. In 2007 and 2008 a large number of tagged individuals prematurely moulted their central retrixes, thus losing the radio-tag. The early moult of the tail feathers affected large number of birds, thus cannot be attributed to the applied methodology. We presume that if breeding and foraging conditions are exceptionally good (characteristic of 2007 and 2008) Red-footed Falcons initiate a suspended full moult in the breeding phase. As the retrix moult pattern of falcons starts with changing the two central tail feathers (FORSMAN 1999), 3 and 8 tagged individuals lost their radio-tags in 2007 and 2008 respectively. Thus, the data obtained from a total of 18 tracked Red-footed Falcons was used in the current study (Table 1).

Birds were individually tracked during the late nesting-period (corresponding to the second half of the nestling stage). A pilot study conducted in 2006 revealed that using triangulations (i.e. assessing the location from fixed positions with simultaneous azimuth readings) is ineffective to assess the position of tracked birds (unpubl. data). Red-footed Falcons have fast traveling speeds resulting in large error polygons moreover, one could only receive signals of the transmitter from a couple of hundred meters when the bird was perched on the ground, making azimuth reading problematic from fixed positions. Therefore, we chose to individually follow the tagged birds.

Two tracking groups – equipped with telescopes and radio tracking equipment (Televilt RX-900 and Yagi antenna) – were assigned to each tracked individual. The first group (observers) remained at

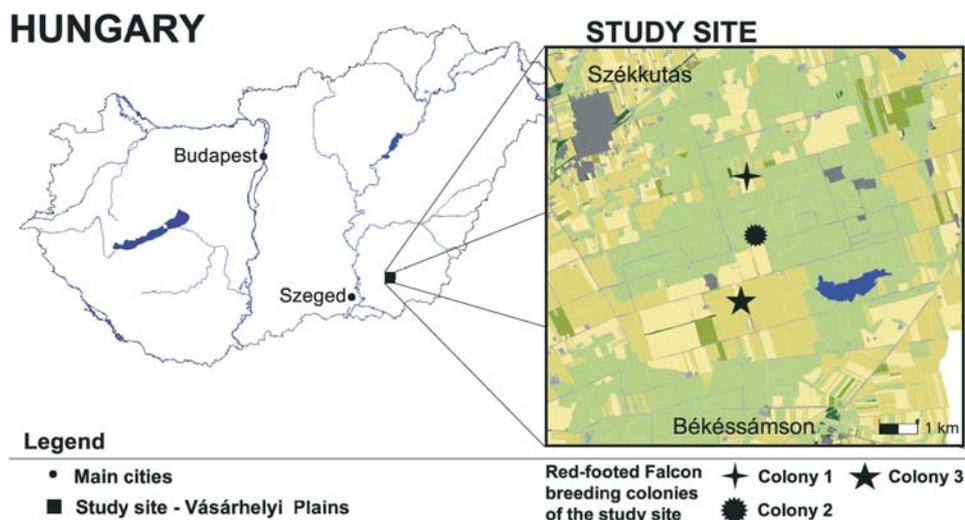


Fig. 1. Location of the study area within Hungary

the nest and recorded the prey delivered, the time the birds left or returned to the nest and informed the second group (followers) on the direction of departure. The observers kept a safety distance of approx. 200 meters to avoid disturbance and to enable unbiased observations of behaviour.

The followers tracked the birds foraging trajectory (the route of the individual from the nest to the foraging area and back) with a four wheel drive vehicle, using the radio-signals to assist visual localization (TELLA *et al.* 1998). Observers continuously informed the followers on the direction of the tracked individual. When visual contact was lost, the two groups triangulated the bird's signal to enable the following group to relocate and continue visual observations.

The within day frequency of prey item delivery to nestlings shows a bimodal distribution with two peaks; the first being in the early morning hours, while the second in the late afternoon (HORVÁTH 1964). To control for this phenomenon, and to avoid bias caused by following easy-to-track individuals we designated two, 4 hour long standard telemetry sessions (time zone: UTC+2); a) morning sessions (4 a.m.–8 a.m.) and b) evening sessions (5 p.m.–9 p.m.). Each tagged individual was tracked for a minimum of 6 (3 morning and 3 evening) sessions. To avoid temporal correlation between sessions we applied a stratified sampling design; for each session the tracked individual was randomly chosen and if possible only one tracking session was carried out on an individual on a given day.

The followers – once visual contact was established – recorded the type of hunting, the effort (number of hoverings, number of strikes, time spent hunting), the success (prey type) and the location at habitat patch level (ID of the habitat patch) of the tracked falcons.

Red-footed Falcons have three distinct hunting types; perch-hunting, hover-hunting, and aerial hunting (prey caught mid-air from near ground altitudes up to cloud base). It is straightforward to link foraging activity to habitat patches in case of the first two hunting types, however in case of aerial hunting this is not possible as prey caught mid-air are presumably originating from large distance and not from habitat patches directly below the bird's location.

We defined a HE as the foraging visit where perch- or hover-hunting was observed at an individual habitat patch, regardless of foraging success. Only one HE was considered if a habitat patch was revisited within the same foraging trajectory to avoid temporal autocorrelation of the data. We hypothesized that the frequency of HEs on a given habitat type allows for a rough estimation of the resource utilization of individuals.

As the current study aims to provide an exploratory analysis on Red-footed Falcon resource selection, only the frequency of HEs in different habitat types were analysed. Further efforts will be made to build more complex resource selection and hunting efficiency models.

Statistical analyses

In contrast with locations obtained with other tracking methods, our data is inherently biased as localization points occurring further from the nest-site are less likely detected. Although a wide variety of home-range estimating methods have been used ranging from α -hulls (BURGMAN & FOX 2003) to parametric (e.g. MATTHIOPOULOS 2003) and non-parametric kernel estimators (GETZ *et al.* 2007) none of these can handle samples that are presumed to implicitly underestimate true home-range extent. Minimum convex polygons (MCP) or convex hulls are known to have adverse properties in home-range estimates as they tend to overestimate true home ranges if a) true home ranges are concave or b) if the location error is large (BURGMAN & FOX 2003). In case of the current study, there are no barriers or inaccessible areas within our study site that may cause concave home ranges, and as only location data of visual observations are included, there is no location error. Therefore, we used 100% MCPs to construct individual home-ranges as these presumably are less likely to underestimate, the true extent of potential foraging areas. Since the location of birds was recorded on habitat patch level, we used the corners of the outermost visited habitat patches to construct the

Table 1. Summary of tracked adult Red-footed Falcons. The first coloumn indicates the year of sampling. The first two characters of the next coloumn (Colony/Sex/ID) refer to the breeding site; SO stands for solitary breeders, C1, C2 and C3 represent the three colonies of the study site, the third character indicates the sex while the last character shows an individual within ID group. Tracking effort summarizes the total of independent sampling events (4 hour long telemetry sessions) and the gross observation time in hours. Number of HEs (hunting events) shows the total number of independent localizations with active foraging. MCP (Minimum Convex Polygons) size shows the 100% (i.e. all localizations included) MCPs in hectares. Only successfully breeding individuals with at least three telemetry sessions were included.

Year	Colony/Sex/ID	Tracking effort No. telemetry sessions/ Gross observation time (h)	Number of HEs	MCP size (ha)
2006	C2♂2	15\60	97	2686
	C2♂1	15\60	158	736
2007	C2♀2	7\28	33	322
	C3♂2	7\28	42	1816
	C3♂5	8\32	68	900
	C1♂3	7\28	46	838
	C1♂2	8\32	136	406
	C3♂6	8\32	39	3431
	C3♂7	8\32	33	1213
	C1♀2	3\12	7	38
	C1♀1	7\28	47	186
2008	SO♂1	7\28	81	1236
	SO♂2	6\24	90	190
	C1♂4	6\24	68	499
	C1♂1	8\32	83	310
	C3♂3	8\32	74	1527
	C3♂4	8\32	36	3467
	C3♂1	7\28	89	1589

MCPs. General linear models (CRAWLEY 2007) were used to analyse inter-colonial and between-sex differences of mean MCP sizes. The dependent variable (MCP sizes) was log-transformed for better model fitting. As there were no females tracked at colony C3 we excluded males from this colony to avoid bias when comparing estimated foraging area size of sexes.

The constructed MCPs were later used to calculate the habitat composition (i.e. the relative size of each previously identified habitat type) of each individual's potential foraging habitat. We observed HEs outside the pre-defined study site in case of two birds (C3♂1 and C3♂6 see Table 1), thus the constructed MCPs protruded the habitat map. These protruding segments compose less than 5% of the individual MCPs, hence we presume that the missing data has no serious effect on the robustness of the analyses conducted.

Table 2. Model parameter estimates of general linear models comparing inter-colonial foraging area size of males breeding in different colonies (Model 1) and inter-sexual differences (Model 2). In Model 1 we analysed the foraging area extent (estimated with individual MCP size) of male Red-footed Falcons as a function of which Colony they breed in. Male individuals breeding at the largest C3 colony had significantly larger foraging areas, compared to males in colonies C2 and C1. In Model 2 we analysed the inter-sexual differences in foraging area extent. We only included males from colonies C2 and C1 to avoid confounding effects of colony size (there were no tracked females from colony C3). Females had significantly smaller foraging areas compared to males. In case of both models foraging area size was estimated with log-transformed individual MCP sizes (ha).

	Variable name	Coefficient	SE	t-value	p-value
Model 1	Colony C3 males' MCP size	1.04	0.36	2.87	0.01
Model 2	Females' MCP size	-1.56	0.61	-2.564	0.03

Model 1 $R^2 = 0.34$, Model 2 $R^2 = 0.36$

We used the Manly selectivity measure to explore global habitat type selection ratios of Red-footed Falcons (MANLY *et al.* 2002). In general, this method compares the available resources to resource usage of populations or individuals. In our case habitat types within individual MCPs (design III type analyses) comprise resource units while HE frequency is the variable describing resource selection. Deviation from random of the global habitat use of all birds was tested with the White and Garrot's χ^2 test (WHITE & GARROT 1990, MANLY *et al.* 2002). We also calculated the population level selectivity ratios (i.e. the average of individual selection ratios) and their confidence intervals (CI) for each habitat type concerned. A habitat type can be regarded as positively selected if the lower CI value of the mean ratio is above, and avoided in case the upper CI value is below one.

Although selectivity measures give a useful overview on the global resource selection of studied individuals, they lack the power of revealing the source of variability. We used a relatively new statistical approach proposed by CALENGE and DUFOUR (2006) to reveal the variability of habitat selection; the eigenanalysis of selection ratios. This tool is considered as an extension of the eigenanalysis (e.g. correspondence or canonical correspondence analysis). In general the eigenanalysis of selection ratios combines the White and Garrot's χ^2 statistics the analysis of selection ratios and a correspondence analysis. The origin of the column space defined by the factorial axes can be considered as the point where a hypothetical animal is using all habitat types randomly or in other words where the White and Garrot's χ^2 statistic is not significant. Individual habitat selection is then visualized within the factorial space describing the available habitats. The amount of overall discrimination is measured by the eigenvalues of the corresponding factorial axes.

We used the R 2.9.0 statistical software (R DEVELOPMENT CORE TEAM 2009) and the package adehabitat (CALENGE 2006) for specific resource selection analyses.

RESULTS

Altogether 1227 independent HEs of 18 birds were analysed. We found large individual variability in home range sizes of radio-tracked Red-footed Falcons (Table 1) with a median MCP size of 838 ha (range 38–3467 ha). Males of colony C3 had significantly larger MCPs compared to the males from colonies C2, C3 and solitary males combined (Table 2, Model 1). Females had significantly smaller foraging areas compared to males (Table 2, Model 2).

Overall foraging habitat selection deviated significantly from random ($\chi^2 = 438.2226$, $df = 43$, $p < 0.0001$). Red-footed Falcons hunted more on grasslands than in the sum of all other habitat types (Pearson's Chi-squared test: $\chi^2 = 307.1$, $df = 17$, $p < 0.0001$) when considering only the total number of observed HEs. However, none of the global Manly selection ratios of the habitat types proved to be significantly positive, only intertilled crops, water surface, reedbeds, woods and artificial surfaces were significantly avoided (Fig. 2).

The performed eigenanalysis of selection ratios revealed a high individual variability of habitat selectivity (Fig. 3). We used the first two factorial axes to perform the analysis explaining altogether 91% of the observed variability. The duality diagram shows that basically two distinct strategies can be identified; the first group of birds favoured grasslands and alfalfa fields while the second group of birds preferred grasslands and cereals. This dual pattern was reflected in the large CI of global Manly's selection ratios of these two habitat types. Only one individual (C3♂7) showed preference towards both alfalfa and cereals, however alfalfa

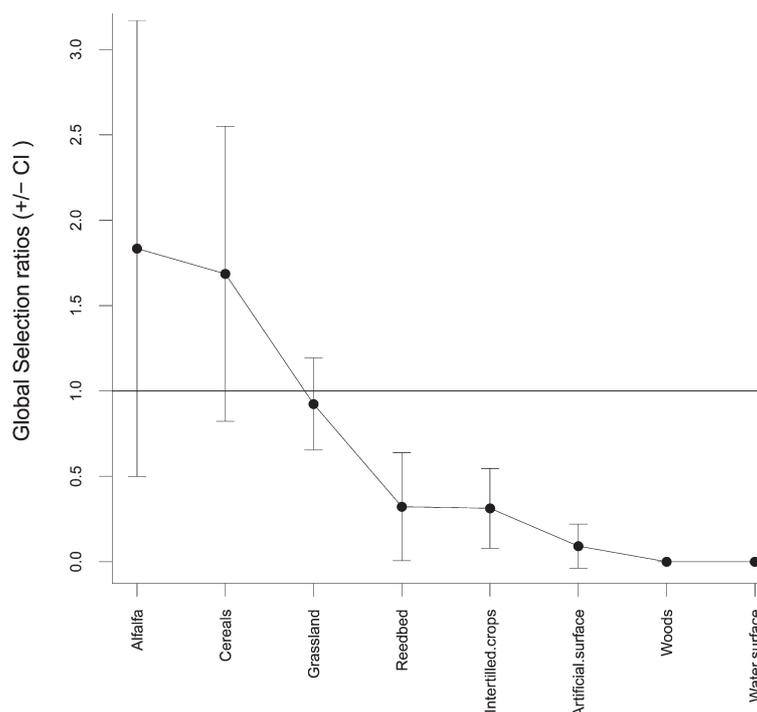


Fig. 2. Global Manly Selection ratios \pm Confidence intervals (CI) of the habitat types analysed. The black dots (●) represent the mean selectivity rate of each habitat type considered. A habitat type can be considered as avoided if the global selection ratio is located in the 0–1 interval, while it can be considered positively selected if larger than 1

preference was more pronounced, thus it was assigned to the later group. The individuals in the two groups cannot be linked to neither colonies, nor years, nor do these groups separate the sexes.

DISCUSSION

The results of this study showed that the foraging area of radio-tagged Red-footed Falcons differs between colonies and sexes (Table 1 & 2), and that these birds have remarkably high overall variability in habitat selection ratios (Fig. 2).

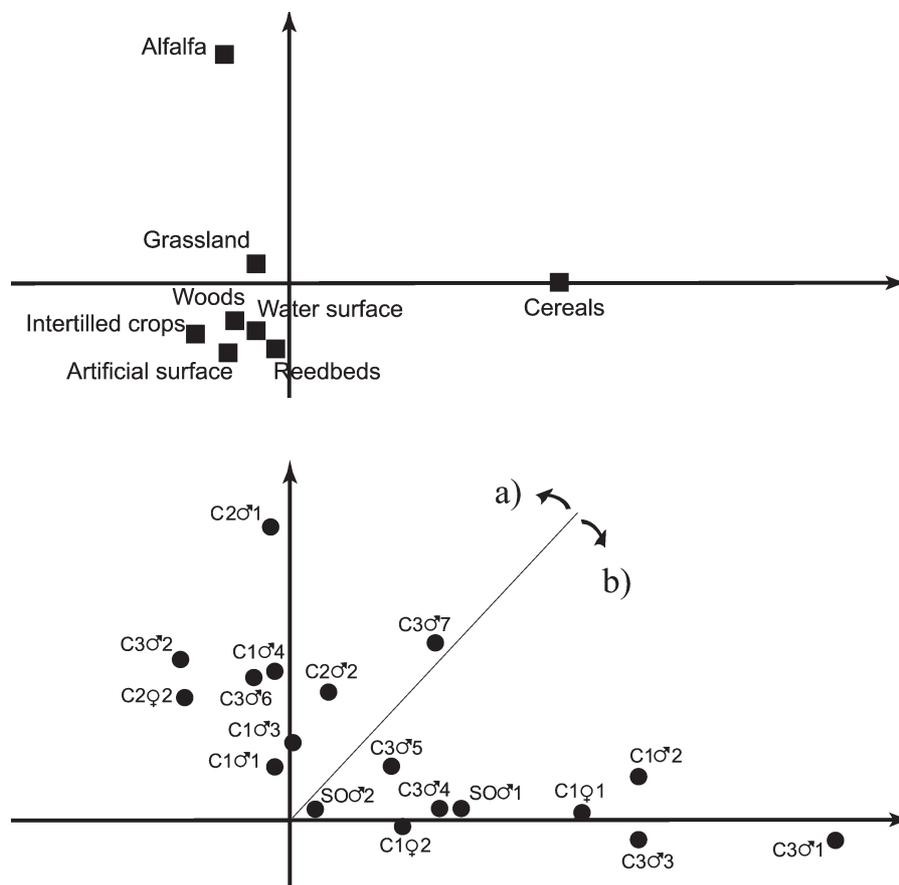


Fig. 3. Duality diagram of the eigenanalysis of selection ratios of radio-tracked Red-footed Falcons. The top figure shows the habitat loadings (■) on two factorial axes, while the lower figure shows the habitat preference of individuals (●) in the same factorial space (see also Table 1). The birds can be assigned to two major groups; a) high alfalfa preference and b) high cereal preference individuals

Median foraging area size is relatively small when considering all tracked individuals, but due to the wide range of this parameter we suggest to use a much larger 3–4 km radius circle when considering potential foraging area of a given Red-Footed falcon colony. This area is likely to cover the bulk of every individuals foraging area, thus can be used for both planning further habitat use related studies and conservation measures.

The most simple explanation of the fact that males breeding in the largest colony (C3) had larger foraging areas may be that the optimal foraging areas were located farther away from this colony. However, intra-specific food competition (e.g. FURNESS & BIRKHEAD 1984, GRIFFIN & THOMAS 2000, AINLEY *et al.* 2004) would result in a similar pattern. Individual fitness may increase with colony size (SERRANO *et al.* 2005, SERRANO *et al.* 2006), hence our results could also indicate that higher quality males breeding in the large colony can utilize foraging patches from larger distances.

The significant difference in MCP size amongst sex groups probably reflects the different role played in parental care, since we found no evidence for sex-specific foraging habitat preference. In small falcons, females are predominantly responsible for offspring protection, while males deliver the majority of prey items (WIKLUND 1990, TOLONEN & KORPIMÄKI 1994, PURGER 2001, SERGIO & BOGLIANI 2001).

Our habitat selectivity analyses indicate that Red-footed Falcons in general avoid foraging on intertilled crops, woods, artificial surfaces, reedbeds and water surface. Intertilled crops in the study area are typically maize and sunflower. These two crops are only harvested in autumn, hence the vegetation structure and height at the time the study was conducted obstructs access to prey (YOSEF & GRUBB JR 1993, SHEFFIELD *et al.* 2001). The avoidance of artificial surfaces like pavements and farm areas is not surprising as these habitats have low prey abundance and are often disturbed. However, the avoidance of reedbeds and water surfaces is of interest, as some of the invertebrate prey item taxa (Odonata and Dytiscidae) of this species (e.g. HARASZTHY *et al.* 1994) are linked to wetlands. We presume that these prey items are predominantly taken while aerial hunting, therefore the foraging location is not linked to the habitat patch. The reproduction of Spade-foot toads – the second most frequent vertebrate prey item – is also linked to wet areas, thus water related habitat types may have an important albeit indirect overall effect on foraging habitat selection.

Our results show that the studied individuals had no significantly positive global preference for any of the available habitat types (Fig. 2). The wide confidence intervals of the estimates yield high individual variability, although Red-footed Falcons used grassland type habitat patches most often for foraging. The latter is in compliance with general expectations and previous large spatial scale

breeding site selection analyses (FEHÉRVÁRI *et al.* 2009). On the other hand, grassland selection was not overall significant as the majority of available habitat types were meadows or pastures.

Partitioning individual habitat preference showed that tracked birds can be clustered into two distinct groups by positive habitat selection (Fig. 3). Intriguingly, Red-footed Falcons in the late nesting period had positive habitat preference towards arable habitat types, but not natural habitats.

The first group predominantly utilised grasslands and mowed alfalfa fields, while the second group could be defined as birds with high cereal preference. Cereals in this case are actually harvested cereal fields, as at the time of the analyses most fields were already harvested. Thus, the primary difference between alfalfa and cereals is probably surface structure and prey item composition. Harvested cereal fields have no or very indistinct vegetation structure, therefore prey detectability is high even when birds perch on the ground. From a surface structure point of view alfalfa fields resemble mown grasslands, presumably with lower prey detectability, but higher prey densities. We found no obvious pattern (sex, year, breeding site) for the birds clustered into “cereals” or “alfalfa” preference groups. Assumably, these results indicate highly individual foraging strategies and further investigation is necessary to fully understand the proximal causes of variability.

The Hungarian National Conservation Plan of Red-footed Falcons (BAGYURA & PALATITZ 2004) was prepared based on the expert opinion of local conservationists working with the species in field. Intriguingly, all experts agreed that the habitat management has to concentrate on grasslands. Our findings are not contradicting previous assumptions since the tracked individuals predominantly hunted in grassland type habitats, but rather demonstrate that certain arable habitat types may have a considerable effect on the species’ foraging habitat selection.

In conclusion, we demonstrated that with optimally chosen tracking methodology and statistical tools, it is possible to reveal the variability of foraging area extent and of habitat selection even when analysing a moderate sample size. The presented results fill in an important knowledge gap on space use patterns of a little known European raptor species of high nature conservation concern.

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