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„Post-fledging dispersal of Western Marsh Harriers (*Circus aeruginosus*): complex movements, behavioural changes and habitat preferences“

verfasst von / submitted by

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For Anita,
I would have liked to discuss Marsh Harrier ecology with you.

Abstract

There are only a few GPS-tracking studies on Western Marsh Harriers (*Circus aeruginosus*) in Europe which deal with large scale movements and migration. However, smaller movements have largely been ignored. Therefore, the focus of this study was the short post-fledging dispersal period after independence from the parents and before the onset of migration. Fourteen nestling Marsh Harriers were equipped with satellite tags to record location and tri-axial acceleration in eastern Austria. These juveniles showed highly variable behaviour regarding dispersal distances, home range sizes and habitat choices. They dispersed up to 167 km from the nest, but when they found suitable hunting areas their home range was relatively small (mean 3.9 km²; 50 % UD dBBMM). 15 days before the onset migration they halted their wide-ranging dispersal and stayed at their temporary settlement areas. A tri-axial acceleration model was used to determine behaviour. Unexpectedly, birds did not increase their hunting efficiency since the energy intensive wing flapping flight slightly increased after independence. In the daily activity cycle, the highest rate of flying (40 %) was reached between 1 PM and 2 PM. Despite natural areas in proximity, all tracked birds moved to agricultural areas and 87 % of the recorded locations fell into this habitat. The most commonly available fields were 'winter cereal' crops, but Marsh Harriers showed little selection for it. The highest preference was shown for fallow land, which indicates bottom-up effects in these biodiversity rich areas to top predators such as the Marsh Harrier.

Key words: Movement ecology, Western Marsh Harrier (*Circus aeruginosus*), Post-fledging dispersal, GPS-tracking, Tri-axial accelerometry, Agricultural habitat choice, INVEKOS, Lake Neusiedl, Raptor

Zusammenfassung

Es gibt nur wenige GPS-Tracking-Studien über die Rohrweihe (*Circus aeruginosus*) in Europa, die sich meist mit großräumigen Zugbewegungen befassen. Kürzere Dispersionsbewegungen wurden jedoch weitgehend ignoriert. Deshalb liegt der Fokus dieser Studie auf der kurzen Zeitspanne nach der Ablösung von den Eltern und vor dem Beginn des Zugs. Vierzehn nestjunge Rohrweihen wurden im Osten Österreichs mit GPS-GMS/GPRS-Satellitensendern ausgestattet. Die Jungvögel zeigten ein sehr unterschiedliches Verhalten in Bezug auf Dispersionsbewegungen, Größe der Home-Range und Wahl des Lebensraumes. Sie entfernten sich bis zu 167 km vom Nest, aber wenn geeignete Jagdgebiete gefunden wurden, war ihre Home-Range (mean 3.9 km²; 50 % UD dBBMM) relativ klein (durchschnittlich 3,9 km²). 15 Tage vor Beginn des Zugs stoppten sie ihre weiträumige Ausbreitung und blieben in ihren temporären Siedlungsgebieten. Zur Bestimmung des Verhaltens wurde ein dreiachsiges Beschleunigungsmodell verwendet. Unerwarteterweise steigerten die Vögel ihre Jagdeffizienz nicht und der energieintensive Aktiv-Flug nahm noch nach dem Unabhängig-Werden leicht zu. Im täglichen Aktivitätszyklus wurde die höchste Flugrate (40 %) zwischen 13 und 14 Uhr erreicht. Trotz der Nähe zu naturnahen Gebieten zogen alle erfassten Vögel in Agrargebiete und 87 % der erfassten Standorte fielen in diesen Lebensraum. Die am häufigsten verfügbaren Felder waren Wintergetreide-Kulturen, für welche die Rohrweihen nur eine geringe Selektion zeigten. Die höchste Präferenz wurde für Brachen festgestellt, was darauf hindeutet, dass auch Top-Prädatoren von diesen Gebieten mit großer biologischer Vielfalt profitieren.

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Introduction

The movement of animals has fascinated people for thousands of years. New technologies such as light-weight GPS tags allow us nowadays to follow animals closer than ever before. This led to the large discipline of movement ecology (Holyoak et al., 2008) with a unifying framework (Nathan et al., 2008). Birds are among the most mobile organisms on earth which has made it difficult to study their movement paths over larger time frames. Only in the last two decades, tags have become small enough to be attached to medium sized birds and durable enough to last over months and years (Sokolov, 2011). Despite this, most studies have focussed on bird migration, whereas dispersal on a smaller scale has largely been dismissed (Holyoak et al., 2008). The decision to move can be seen as the behavioural response to external cues and the internal state of individuals (Serrano, 2018). Natal dispersal (also known as juvenile dispersal) is a crucial phase in the life of long-lived birds, such as raptors (Engler & Krone, 2022; Greenwood & Harvey, 1982), in which they make undirected exploratory flights (Newton, 2010). It involves three distinct steps: a decision to leave the natal area (emigration), a floater phase and to end natal dispersal, and the establishment of a territory (Balbontín & Ferrer, 2005; Clobert, 2003). The reasons for dispersal are still very much debated and are probably multicausal (Matthysen, 2012). Some proposed theories for the ultimate cause of dispersal are kin selection theory (disperse to avoid kin competition and inbreeding), bet hedging (disperse to increase variance in offspring fitness) or to escape unfavourable environmental conditions (Serrano, 2018). These factors seem to outweigh the costs associated with moving through unfamiliar and potentially unsuitable terrain where birds are exposed to unknown threats (Matthysen, 2012).

In migratory birds, such as the study species, the Western Marsh Harrier (*Circus aeruginosus*, hereafter Marsh Harrier (Fig. 1)), the first calendar year can be divided into five distinct life phases: nestling, post-fledging dependency period, post-fledging dispersal period (and start of natal dispersal), migration, and wintering (Wiens et al., 2006; Kitowski, 2004; Bustamante & Hiraldo, 1989). The breeding distribution of this medium sized raptor species stretches from the Iberian Peninsula in the west to Central Mongolia in the east, and from 65° N in Siberia to 33° N in Afghanistan and Northern Africa (BirdLife International, 2022; Orta et al., 2020). The species is listed as ‘Least Concern’ and in Europe its population is currently increasing (Orta et al., 2020). However, in some countries there are conservation concerns. For example, according to the Austrian Red List, it is listed as ‘Near Threatened’ and in the list of species of conservation concern it is classified as an ‘amber’ species and thus has priority for conservation measures (Dvorak et al., 2017). Moreover, it is a species listed in Annex I of the EU Birds Directive (‘Directive 2009/147/EC of the European Parliament and of the Council of 30 November 2009 on the Conservation of Wild Birds’, 2010). The Austrian breeding population holds 350 to 500 pairs with a stable short-term trend; the long-term trend is positive (Dvorak, 2019). Threats include illegal persecution (Schmidt, 2022), pesticides and agricultural intensification (Dvorak et al., 2017;

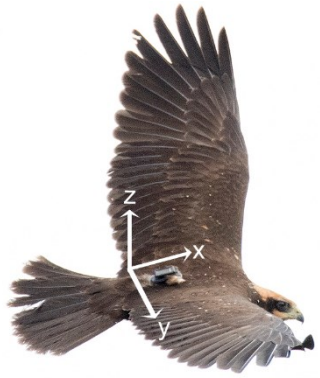

Figure 1: The study species, Northern Marsh Harrier (Circus aeruginosus) in juvenile plumage. Note the 10 g satellite tag on the lower back with raised solar panel. The white arrows indicate the three acceleration axes (x: surge; y: sway; z: heave). The individual shown is 'Dagoberta' in the post-fledging dependency period shortly after leaving the nest.

Gamauf, 1991). The NGO BirdLife Austria is currently engaged in a species conservation initiative (https://www.birdlife.at/page/telemetrie-rohrweihe; Schmidt, 2022), of which this study is a contributing component. So far, there have only been a few studies conducted on Marsh Harriers in Austria. Those studies have investigated breeding densities (Wendelin, 2019; Dvorak et al., 1997; Sezemsky & Ripfel, 1985; Sezemsky, 1983) and habitat use (Gamauf & Preleuthner, 1996; Gamauf, 1993) at Lake Neusiedl.

The migration of Marsh Harriers has been studied via GPS tracking in southern Sweden (Vansteelant et al., 2020; Vardanis et al., 2011; Klaassen et al., 2010; Strandberg et al., 2008), Belgium and the Netherlands (Spanoghe et al., 2022; Vansteelant et al., 2020; Milotic et al., 2020) and Hungary (Váczi, 2020). Current studies are taking place in the Czech Republic, Slovakia (Ivan Literák, pers. comm.) and Austria (BirdLife Austria, unpublished data). Most of the central and northern European breeders migrate to sub-Saharan West Africa (Vansteelant et al. 2020; BirdLife Austria unpublished data), whereas western European breeders are more sedentary (Sternalski et al., 2008).

Tri-axial accelerometry is a remote sensing technology that has proven to be a useful tool to study behaviour remotely in tagged individuals (Brown et al., 2013; Nathan et al., 2012). The acceleration measurements in three dimensions (Fig. 1) at a high frequency allow to be translated back into different types of animal movements inferring behaviour. Tri-axial accelerometry data has been used to distinguish between different flight types of wild raptors (Order Accipitriformes and Falconiformes), e.g. Lesser Kestrels (*Falco naumanni*) (Hernández-Pliego et al., 2017), Andean Condors (*Vultur gryphus*) (Williams et al., 2015), and Eurasian Griffon Vultures (*Gyps fulvus*) (Nathan et al., 2012) and in trained, captive Eurasian Griffon Vultures, Himalayan Vultures (*Gyps himalayensis*), Tawny Eagles (*Aquila rapax*), and Harris's Hawks (*Parabuteo unicinctus*) (Williams et al., 2015; Duriez et al., 2014; Halsey et al., 2009). Harriers (Genus *Circus*) are good study organisms for the interpretation of acceleration data as their hunting behaviour follows the same routine of wing flapping behaviour with short glides and sudden drops for prey (Simmons, 2000; Clarke, 1995). This work uses acceleration data in combination with videos, showing different behaviours of Marsh Harriers in the field, to train and re-evaluate acceleration models as proposed by Shamoun-Baranes et al. (2012).

In this study, the dispersal behaviour and habitat use of juvenile Marsh Harriers in the post-fledging dispersal period using GPS, accelerometry and habitat data was investigated. It is one of a few studies that deals with the post-fledgling dispersal in detail. This period starts after the

post-fledging dependency period and ends with the onset of the first migration (Newton, 2010). There is no clear terminology for this phase and it is also known as post-dependent dispersal (Hill et al., 1999) and, more generally, as pre-migration autumn movements (Strandberg et al., 2008) or post-breeding dispersal (Witkowski, 1989). In some cases, the parent-dependent and the following independent phase are put together as post-fledging movement (Sternalski et al., 2008; Beske, 1982), although they differ considerably in movement patterns and behaviour. The parent-dependent fledging phase is also known as the post-fledging phase (Newton, 2010). However, to distinguish it from post-fledging dispersal, the term post-fledging dependency period will be used (Kitowski, 2002).

This post-independence period, as the initial phase of natal dispersal, is a crucial phase in the life history of raptors as they are still vulnerable and naive (Newton, 1979), which leads to a high mortality and has only been studied poorly (García-Macía et al., 2022). In radio tagging studies from the 1980s to the early 2000s, it was difficult to follow the birds with the necessary antenna once they left the immediate nesting area (Sternalski et al., 2008; Bavoux et al., 1998; Beske, 1982). Only Bavoux et al. (1998) and Sternalski et al. (2008) have examined this time period with radio-transmitters in sedentary populations of Marsh Harriers in France. Additionally, some post-fledging dispersal movements were shown in an Argos-tracking study in Sweden (Strandberg et al., 2008).

In this study, home range size and daily activity patterns of Marsh Harriers in their post-fledging dependency period will be described to enhance the fundamental understanding of this charismatic species. The daily activity patterns were described as bimodal with peaks in the morning and evening hours (Gamauf & Preleuthner, 1996). The same pattern was described by Witkowski (1989) for food provisioning early in the nestling season with one (flat) peak distribution seen later in the nestling season. The three populations studied in this work occur across a gradient from natural area to intensive farmland.

This study proposes several hypotheses concerning the outcomes for the short post-fledging period. I expect that birds from more natural areas with higher prey abundance use smaller home ranges and tend to move less compared to birds in homogenous agricultural areas (Tucker et al., 2019; Dodge et al., 2014).

With the optimal foraging theory in mind, which predicts that individuals should optimise foraging in terms of time and energy expenditure (MacArrthur & Pianka, 1966), I expect that flapping behaviour with high energetic demand (Duriez et al., 2014) will decrease with more experience, as the studied juvenile Marsh Harriers are inexperienced hunters. Furthermore, I hypothesise that daily travel ranges will increase after independence but will then stop when a suitable hunting area is found. Prior to migration, I anticipate less dispersive movements as suitable hunting grounds should have been found by then.

This work also presents a detailed characterisation of agricultural habitats preferred for foraging in juvenile Marsh Harriers which will efficiently guide conservation measures for this species.

Methods

Field work and study sites

The study was carried out in eastern Austria, where the main stronghold of Marsh Harriers in Austria is located (Probst & Suanjak, in prep.). Starting in May 2021, Marsh Harrier pairs and possible nest sites were observed from nearby vantage points and by triangulation the approximate location of the nest was estimated. Nest surveys to determine the age of the nestlings were undertaken with drones to keep disturbance at a minimum and not to cut paths through dense vegetation to minimize predation risk (Hardey et al., 2013). Necessary permits to enter core National Park areas, for drone flights and bird ringing and tagging were issued by the Federal State of Burgenland (A4/AR.JA-10106-12-2021, A4/NR.AB-10063-5-2021) and Lower Austria (GFL2-J-107/028).

Three study sites were used: the reed belt at Lake Neusiedl near the Zitzmannsdorfer Wiesen (47.8860, 16.8469; part of the National Park Neusiedler See-Seewinkel); Hohenau an der March (48.5927, 16.9073) and Hausbrunn (48.6188, 16.8399) (Fig. 4). The latter two locations are secondary habitats; in Hohenau, the artificial ponds were used by a sugar refinery plant but are now managed by a local conservation organisation (Auring). The artificial ponds in Hausbrunn are from a small sewage treatment plant. The nests were located mostly in reed (*Phragmites australis*) and in one case in typha (*Typha* sp.) beds. The surrounding areas of the three study sites form a gradient from natural areas to intensive agriculture: The studied population at Lake Neusiedl lies in a national park (Neusiedler See-Seewinkel) with the highest Marsh Harrier population in Austria. The studied population in Hohenau is located in the March-Thaya flood plains that harbour a relatively high proportion of meadows and fallow land with adjacent high-intensity agricultural areas. In this human-dominated habitat, the third studied population (Hausbrunn) occurred.

A total of 14 juvenile Marsh Harriers were tagged in the nest shortly before fledging between the 7th and 13th of July 2021 with 10g GPS-GMS/GPRS tags from the company Ornitela (Fig. 1). After the tagged Marsh Harriers left their nests, I followed them to get video footage of their behaviour while the tags continuously took tri-axial acceleration measurements. The camera setup used was a Nikon D500 DSLR with a Tamron 150-500 mm f5-6.7 lens and videos were taken with a vertical resolution of 720 pixels (HD). Finally, 169 minutes of video footage of nine different birds showing different behaviours were obtained (Appendix 1). All pictures presented in this study have been taken by the author.

Tracking time frame and GPS tags settings

Of the 14 tagged juvenile Marsh Harriers, two birds died before the onset of migration and one lost its GPS tag within a couple of days after fledgling. One male (‘Cosmo’) started its migration without dispersal phase. These four individuals have been excluded from the analysis, except for

the migration onset date and independence date of ‘Cosmo’. Of the remaining ten birds, seven were females and three males, determined by body weight, bill and claw length (Bavoux et al., 2006; Bijlsma, 1997), from five different nests. Birds have been named by the order of tagging (beginning with the letter ‘A’) and juveniles from the same nest were named with the same initial letter (Tab. 2).

Defining the exact moment from which fledglings are independent from their parents (and thus the onset of post-fledgling dispersal) from GPS data is difficult, as this can be seen as a progressive process in which offspring become increasingly detached from their parents (Cadahía et al., 2007). In this study, the start of the post-fledgling dispersal was defined as the first night which was spent > 3 km from the nest site (Wiens et al., 2006). This usually corresponded to a larger home range size and to siblings splitting up. The onset of migration is straightforward to define, as birds leave the area in a direct path towards SSW in the morning (Fig. 4, Fig. 7; Strandberg et al., 2008). The cutoff points were set at midnight, resulting in only complete days being considered.

The GPS and acceleration data used in this study are available on Movebank (movebank.org, study name "Circus aeruginosus_Summer 2021 Acceleration”) and some individuals can be publicly followed on BirdLife Austria’s project page: https://www.birdlife.at/page/telemetrie-rohrweihe.

The GPS tags were programmed to take GPS locations as frequently as possible depending on the battery status throughout the day and at a set interval of four hours at night, resulting in a mean GPS fix interval of 4.4 minutes during the day and 62,885 GPS locations (median 6,645 per individual). After each GPS fix, the tag was programmed to record 10 Hz tri-axial accelerometry data continuously for 60 seconds.

Statistical analysis

The statistical analysis was performed in R (R Core Team, 2021) and the spatial analysis relied on the packages move (Kranstauber et al., 2022), adehabitat (Calenge, 2006) and amt (Signer et al., 2019). Figures 3 and 4 were produced in QGIS 3 (QGIS.org, 2023) with Google Maps satellite view as background map. Daily sunset and sunrise times were taken from the website https://www.sunrise-and-sunset.com/ for the location of Gänserndorf (48.3397, 16.7148) as the function ‘sunriset’ of the maptools package (Bivand & Lewin-Koh, 2022) did not deliver satisfactory results.

Accelerometry model

The tri-axial accelerometry data was analysed using the software Firetail and its artificial intelligence model FireSOM to classify acceleration data (Berger et al., 2022). The settings and structure of the model can be found in Appendix 2 and 3. One half of the video footage of the Marsh Harriers was used to train the model and the other was used to test the fit of the model.

Ultimately, four behaviour categories were distinguished: inactive ground (resting birds which are mostly on the ground but not exclusively); active ground (walking, feeding or preening mostly on the ground but not exclusively); active flight (at least one wing flap in a four to five second window) and inactive flight (gliding, soaring). To describe the fit of the model, four descriptive metrics were calculated: accuracy describes the overall correctness of the model; precision is a function of true positives and false positives; recall describes how many times the model was able to detect a specific category and the F1-score is an overall metric to describe the model accuracy from recall and precision (Sokolova et al., 2006). Overall, the model performed well (average F1 score: 0.93; Tab. 1).

Table 1: Overview of the performance of the tri-axial acceleration model to predict four behaviour categories in juvenile Marsh Harriers.

category	modus	accuracy	precision	recall	F1-score	sample size (n)
inactive flight	test	0.97	0.78	0.62	0.69	37
	training	0.93	0.87	0.87	0.87	220
active flight	test	0.97	0.95	0.99	0.97	349
	training	0.94	0.92	0.95	0.93	302
inactive ground	test	0.98	0.96	0.99	0.98	378
	training	0.98	0.97	0.95	0.96	131
active ground	test	0.96	0.81	0.57	0.67	37
	training	0.95	0.92	0.89	0.90	168

The settings of the GPS tags were initially set to record 60 seconds of 10 Hz tri-acceleration recording after each GPS location in the online interface. Due to inaccuracies in the technology of the tags, the tags recorded at a frequency of 12 Hz and split the records into four to five second (81 % of events) long acceleration bursts, which were separated by a one second pause (presumably to store the data). Each of the acceleration bursts was assigned to one of the above mentioned categories with the FireSOM model of Firetail.

Day travel range and displacement

All distance and area calculations were made using the ETRS89-extended / LAEA Europe (EPSG: 3035) projection. The displacement was calculated using the 'Net Squared Displacement' which is the squared distance between the start location and each subsequent location (Singh et al., 2016; Calenge, 2006). This scale is often used to characterise coarse movement patterns (Bastille-Rousseau et al., 2016).

The daily distance covered by each individual was calculated as the 'day travel range' (dtr) which is the longest side of the smallest rectangle which encompasses all locations of one day (Steiniger & Hunter, 2013). This has the advantage that sample size does not influence the result as much compared to calculating the sum of the distances between locations for a given day. A further advantage is that it makes long distance movements more visible.

Utilisation distribution

The individual Marsh Harrier's Utilisation Distribution (UD), quantifying the probability density that a bird will occur at a given point in space, was calculated using a dynamic Brownian Bridge Movement Model (dBBMM) with margin size 11, window size 23, and time step set to minimum time interval and raster size to 100 m (Kranstauber et al., 2012). The dBBMMs UDs were summarised at 50 % and 95 % levels. Compared to other UD methods, the dBBMM is less sensitive to irregular sampling as it takes both the time differences between locations and the trajectory of the path into account (Kranstauber et al., 2012). To compare differences in sizes of the 50 % and 95 % UDs between locations and sexes, a one-way ANOVA, and an unpaired t-test respectively were used. Normality was checked with the Shapiro-Wilk test and homogeneity with the Levene test (de Winter, 2013).

Habitat analysis

For the Resource Selection Function (Avgar et al., 2017) the agricultural habitat was taken from the INVEKOS layer (Agrarmarkt Austria, 2022). The INVEKOS system is an important administrative tool of agricultural areas in Austria on which many subsidies depend on. The system is updated every year and is published open access in the subsequent year. Every plot of land is assigned to a crop category and some other features surrounding the agricultural areas are also included. The underlying 113 original INVEKOS categories have been merged to 33 categories and translated to English (Appendix 4).

As the INVEKOS layer only covers Austria, the GPS points and 95 % UDs have been clipped to the extent of Austria. Four Marsh Harriers that spent most of their time in neighbouring countries were excluded from the analysis ('Beate' in HU, 'Dorian' in CZ, 'Fatime' in CZ, 'Gustav' in HU). Following Fieberg et al. (2018) for every GPS fix of every individual, 20 random locations were generated in the respective 95 % UD. If locations did not fall into the INVEKOS layer (e.g., forests, gardens, streets) they were assigned to the 'non-agri' category. Every used point was weighted 1 and every random point 5000 (Fithian & Hastie, 2013). A Generalised Linear Model (GLM; family: binomial) was fitted with the categorical covariates taken from the INVEKOS polygon layer for each individual, because each had a unique set of habitats available. The category with the highest availability was winter wheat and it showed a consistent low preference over all individuals. Therefore, it was chosen as the reference category for the GLMs. A weighted mean for every habitat category of all exponents of the different GLMs was taken but coefficients with an estimated standard error greater than 10 were removed as outliers.

Results

Home ranges and time frames

The median start day of independence was 15th August 2021 (n = 12, range = 9th-26th August 2021) and the median start day of migration was 19th September 2021 (n = 11, range = 25th August - 8th October 2021), leaving a time frame of median 33 days (n = 11) as post-fledging dispersal phase (Tab. 2). 'Enea' started its migration on 1st of October 2021 over the Alps but returned to the initial area on the same day. The next day it was successful in starting the migration. Therefore, October 2nd has been chosen as its date of migration onset. Two of 13 birds died between fledging and the onset of migration, resulting in a survival rate of 85 %. The farthest distance from the nest was reached by 'Dorian' with 167 km towards the northwest, on the opposite side was 'Cosmo' who started its migration early and straight from the nesting site (Tab. 2).

Table 2: Overview over all GPS-tagged juvenile Marsh Harriers. Explanation of the variables: birdname: Name of the individual (same initial letter indicates individuals from the same nest); sex: m = male, f = female; independence date: start date of post-fledging dispersal period; migration date: date of migration onset; n.days: duration of the post-fledging dispersal period in days; n.GPS.locations: number of GPS locations; mean.dtr: mean day travel range; 95 % UD: area [km²] of the 95 % Utility Distribution (dBBMM); 50 % UD: area [km²] of the 50 % Utility Distribution (dBBMM).

location	birdname	sex	independence date	migration date	n days	n GPS locations	mean dtr	95 % UD [km²]	50 % UD [km²]
Lake Neusiedl	Abdul*	m	15 August 2021						
	Beate	f	12 August 2021	8 October 2021	56	5214	6.9	7.8	0.36
	Bela*	m							
	Branco	m	9 August 2021	26 September 2021	47	6075	5.3	25.2	2.06
	Gustav	m	12 August 2021	19 September 2021	37	8180	7.6	10.4	0.6
Hohenau	Cleopatra	f	29 August 2021	19 September 2021	20	928	10.5	52.9	5.78
	Cosmo*	m	25 August 2021	25 August 2021					
	Dagoberta	f	16 August 2021	19 September 2021	33	7456	7.2	15.2	0.88
	Dorian	m	15 August 2021	13 September 2021	28	4710	43.0	50.9	2.29
Hausbrunn	Eleonora	f	26 August 2021	21 September 2021	25	4508	12.0	102.9	5.6
	Emilie*	f							
	Enea	f	21 August 2021	2 October 2021	41	11555	22.9	214.7	5.77
	Fatime	f	15 August 2021	28 September 2021	43	10099	47.4	138.2	8.23
	Fredi	f	26 August 2021	18 September 2021	22	4160	18.7	106	6.1

Footnote: * Life histories of individuals with missing data: 'Abdul' was found dead 12 km from the nest on 18th of July 2021 (probably predation); 'Bela' lost its GPS tag near the nest; 'Cosmo' migrated early without dispersal phase; 'Emilie' was found dead 180 m from the nest shortly after fledging (probably predation).

The home ranges, described as 95 % and 50 % Utility Distributions (UD), also varied widely with a mean of 51.9 km² for 95 % and 3.9 km² for 50 % UD, with a range of the factor 17.7 (95 % UD) and 22.9 (50 % UD) between the smallest and largest. The 95 % UD differed significantly between the three study locations (one-way ANOVA: $F_{2,7} = 12.11$, $p = 0.005$, Fig. 2). While the 95 % UDs of Hohenau and Hausbrunn (Tukey posthoc Test: adj. $p = 0.02$) and of Lake Neusiedl and Hausbrunn (Tukey posthoc Test: adj. $p = 0.006$) differed significantly, there was no significant

difference between Lake Neusiedl and Hohenau (Tukey posthoc Test: adj. $p = 0.69$) for the same UD. The area of the 50 % UD showed only a significant difference between Lake Neusiedl and Hausbrunn (one-way ANOVA: $F_{2,7} = 9.81$, $p = 0.009$ and Tukey posthoc Test: *adj.* $p = 0.008$). There was no difference between the sexes in relation to mean home range sizes in both 50 % UDs and 95 % UDs (t-test $p = 0.13$ for 50 % and t-test $p = 0.2$ for 95 %). The 50 % UD was comparatively small, compromising a mean of only 6 % of the 95 % UD area (Tab. 2) but still overlapped partly in some birds (Fig. 3).

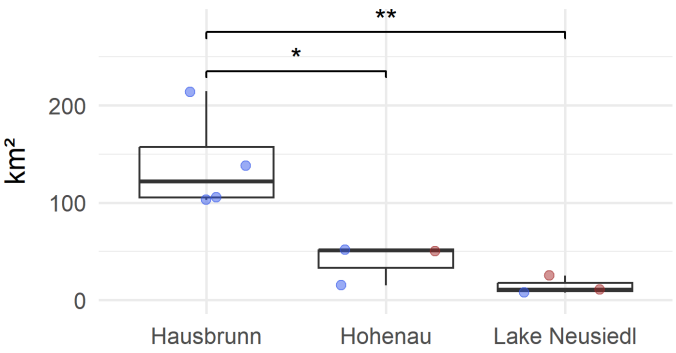

Figure 2: Boxplot of 95 % UDs (dBBMM) grouped by different locations. Bars between plots indicate significance levels (p < 0.05, ** p < 0.01). Blue dots are indicating females and red dots males.*

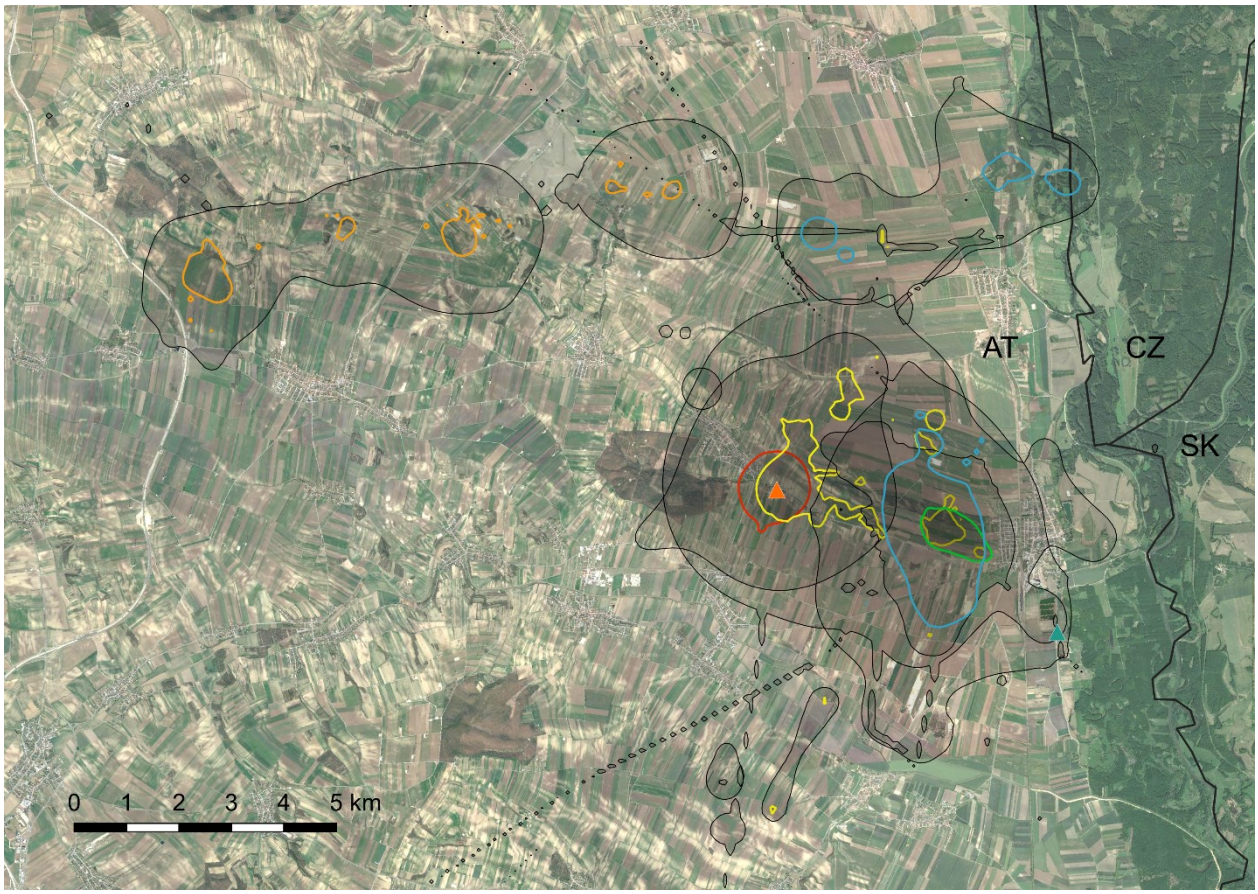

Figure 3: Example of space use on a small scale of five different juvenile female Marsh Harriers from two different tagging locations. Grey areas are 90 % Utility Distributions, coloured lines are 50 % Utility Distributions. Triangles depict tagging locations (orange = Hausbrunn, blue = Hohenau). Coloured lines: orange = Eleonora, yellow = Enea, red = Fredi, blue = Cleopatra, green = Dagoberta. Black lines are country borders (AT = Austria, CZ = Czech Republic, SK = Slovakia).

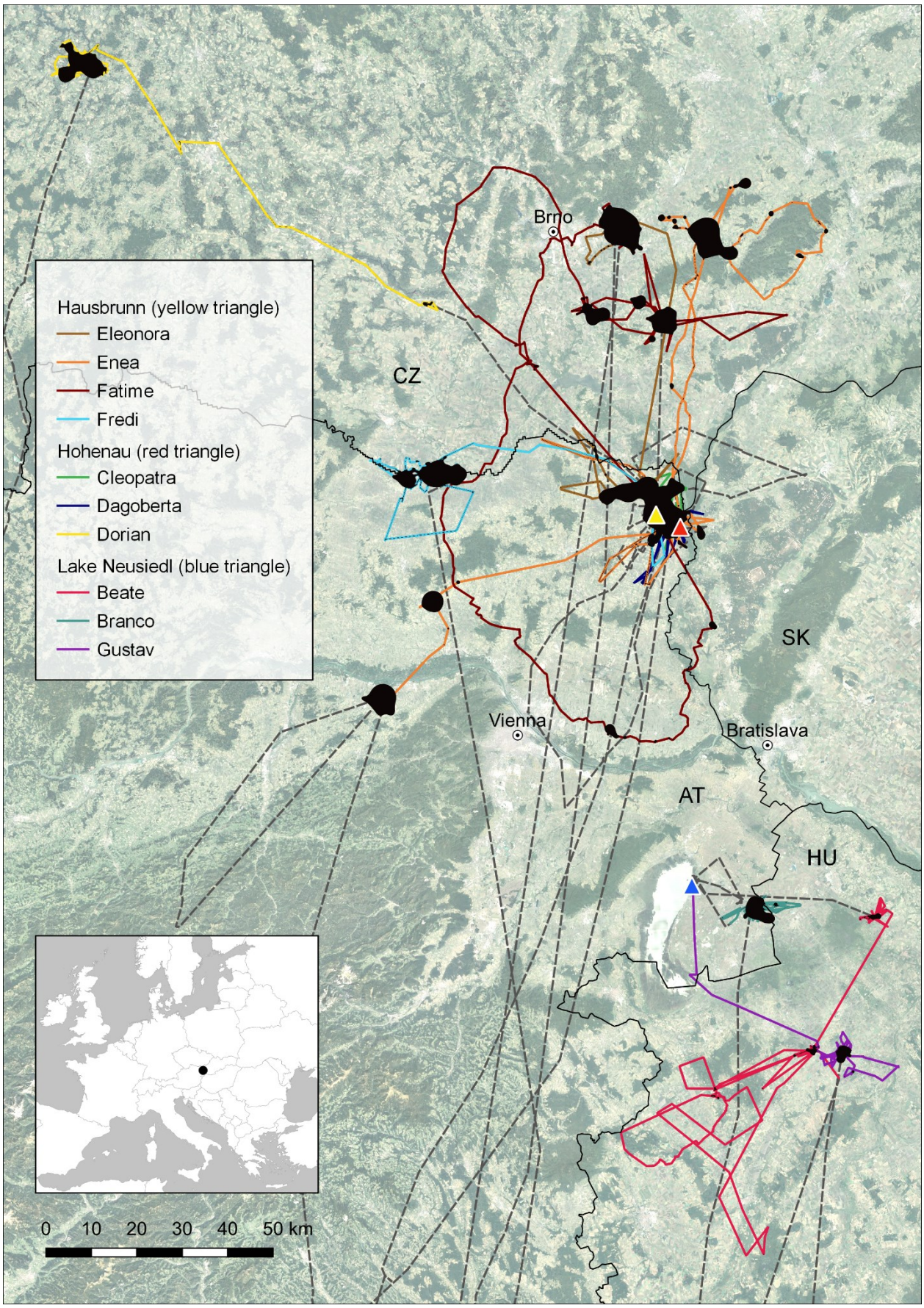

Figure 4: Overview over all tracks. Grey dashed lines depict movement which was not part of this study (non-independent fledglings and migration). Black lines are country borders (AT = Austria, CZ = Czech Republic, SK = Slovakia, HU = Hungary). Insert shows the location of the study within Europe.

Changing behaviour during post-fledging dispersal

The behaviour of juvenile Marsh Harriers did not show any distinctive changes over time (Fig. 5a). Only the last 15 days before the onset of migration were marked by an increase in 'inactive ground' and a decrease in 'active flight' behaviour (Fig. 5c). The 'active flight' category did not decrease after the independence from the parents but showed a slight increase which drops after 12 days (Fig. 5b).

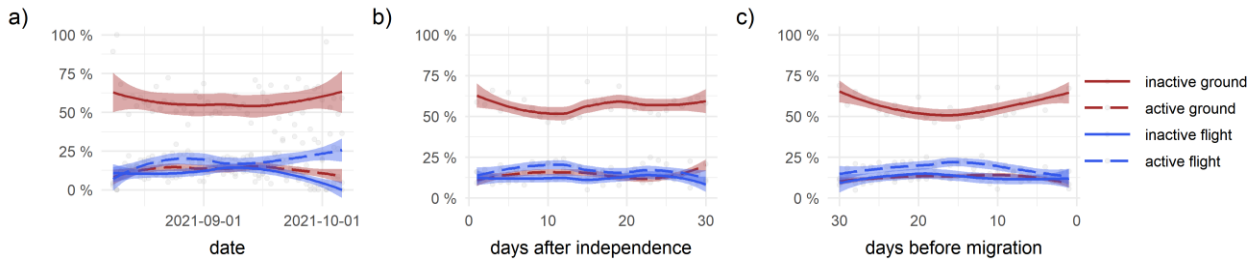

Figure 5: Proportions of different behaviour classes on the daily time budget on different time scales. Ribbons show confidence intervals and grey dots the actual proportion of each behaviour for each day of each individual. Note that 5c has the x-axis inverted to have later days intuitively on the right and that 5a has small sample sizes in the start and the end days due to individual differences in the time frames considered.

Day travel range and displacement

The highest mean day travel range (dtr) was reached in the first half of September (Fig. 6a). After independence the dtr stayed relatively constant (Fig. 6b) but showed a steady decrease starting 18 days before the onset of migration (Fig. 6c).

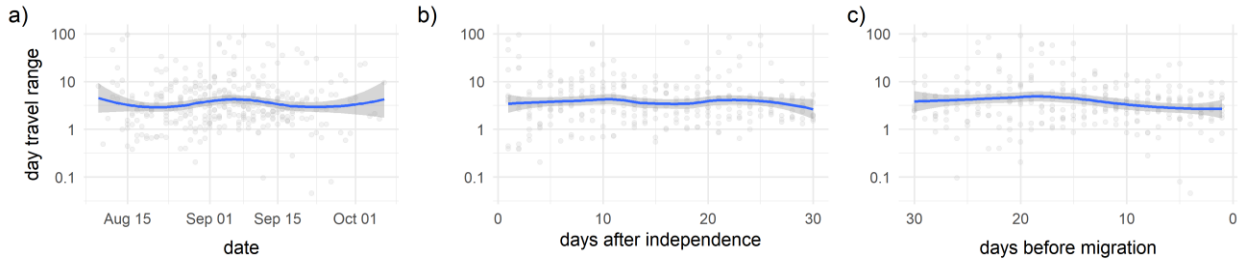

Figure 6: Variation of day travel range (dtr) on different time scales. Grey ribbons show confidence intervals and grey dots the actual dtr of each individual. Due to individual differences in the time frames considered, 6a has small sample sizes in the start and the end days. Note that the y-axis is log-transformed and 6c has the x-axis inverted to have later days intuitively on the right.

The net squared displacement shows clear long-distance movements and then relatively little movement once settled (Fig. 7). The nest location (y = 0) was rarely visited after independence. There is no clear pattern visible in Figures 7a and 7b, but interestingly the last 15 days before the onset of migration were spent at the same temporary settlement area (Fig. 7c).

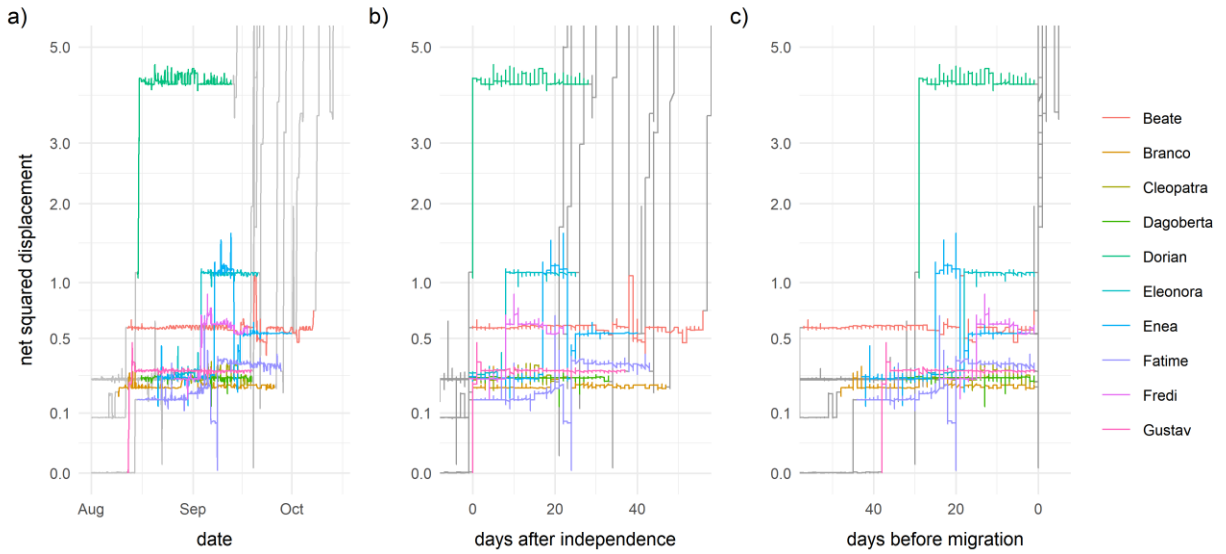

Figure 7: Net squared displacement on different time scales. Grey lines indicate the days before post-fledging dispersal and migration respectively. Note that the y-axis is square root transformed and the x-axis of 7c is inverted to have later days intuitively on the right.

Daily activity cycle

The daily time budgets determined by an acceleration model showed the expected pattern of higher activity during the middle of the day. The 'inactive ground' category showed a surprisingly high proportion (> 47 %), meaning that juvenile Marsh Harries sit still most of the time. The 'inactive flight' category shows a clear pattern of rising between 8 AM and 11 AM and then reaching a high plateau until 3 PM when it drops down again until 7 PM. The other flight category 'active flight' shows a similar pattern, but not as clearly demarked as 'inactive flight' with higher values in the early morning and late afternoon hours (Fig. 8). Overall juvenile Marsh Harriers were most airborne between 1 PM and 2 PM, reaching a mean value of 40 % (Appendix 5). Note, however, that these values were measured in central Europe during chiefly August and September (CEST) and due to shifting sunrise and sunset times these values are different in other seasons.

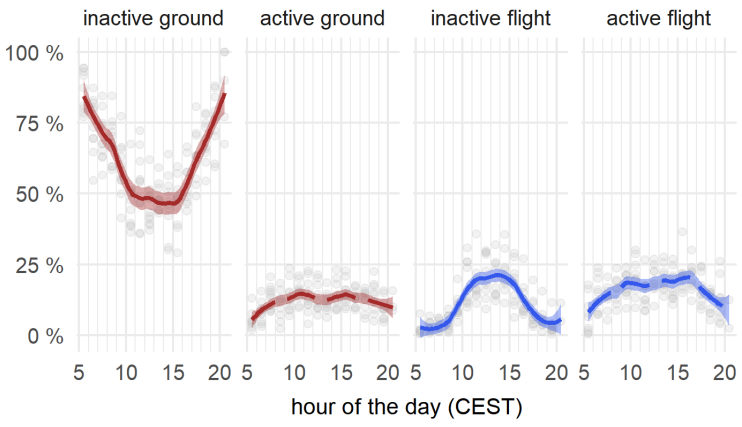

Figure 8: Proportions of different behaviour classes during daytime hours determined by a behaviour model from acceleration bursts.

Habitat use and selection

Only a mean of 14.2 % of the random locations calculated in the 95 % UDs fell into the 'non-agri' category, meaning that 85.8 % of locations were covered by the INVEKOS layer.

Winter cereals (mostly winter wheat *Triticum aestivum*) which were already harvested by the start of the post-fledging dispersal were the most common crop available in the UDs of all birds and this habitat was naturally well used but selection for it was weak. The 'non-agri' category was also widely available but did not show a clear pattern of selection. Most individuals showed highly variable preferences of habitats, only 'Fredi' showed a pattern of using the available categories proportionally but with avoidance of 'winter cereals' and a preference for 'fallow land' (Fig. 9).

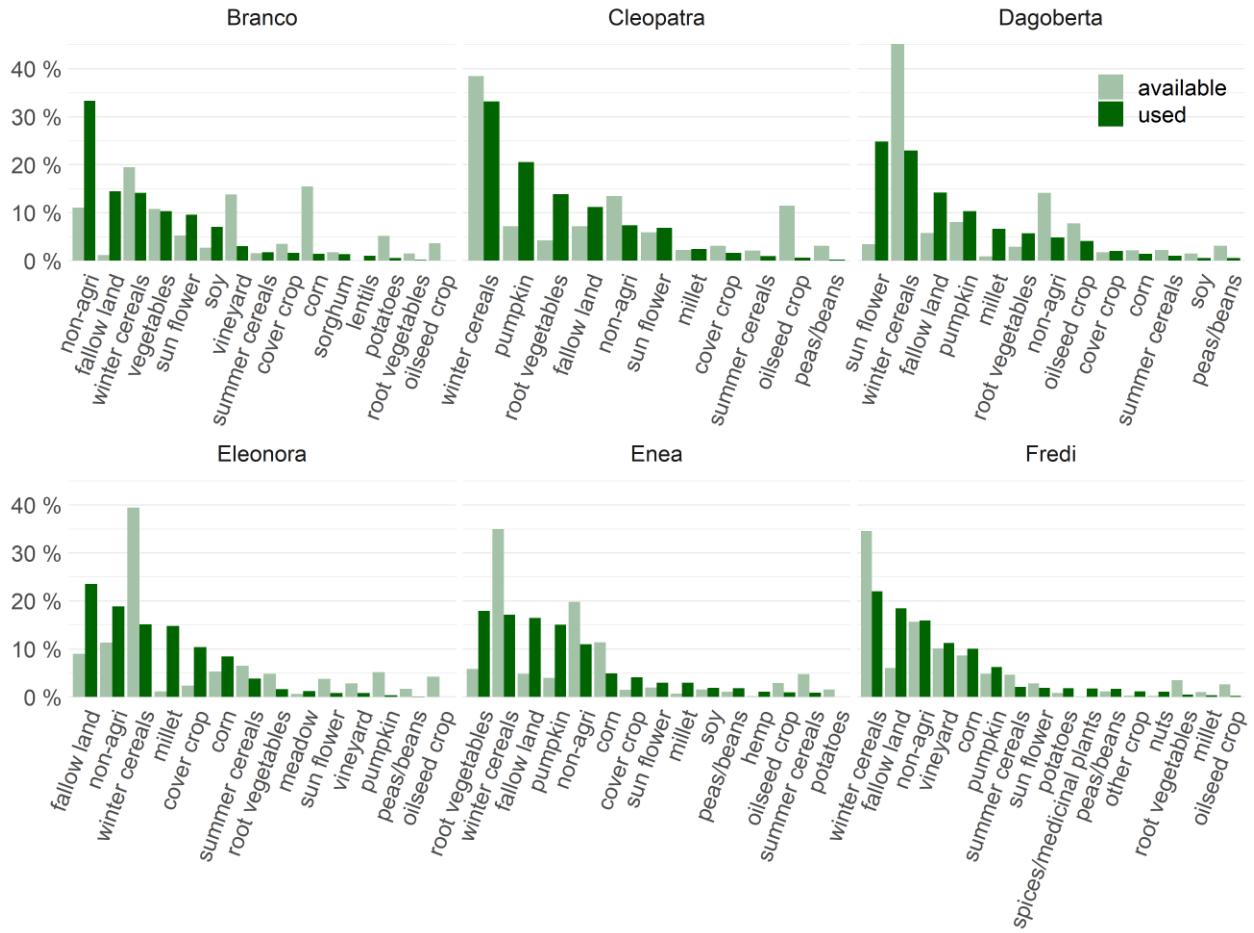

Figure 9: Proportion of used vs. available agricultural habitat, sorted by use for each individual. Pale green bars are available and dark green bars are used agricultural habitat. Selection is the difference between the bars and use is the size of the bars. Note that different birds had different habitats available and habitats with a frequency of < 1 % for both available and used categories were excluded in the graph.

The large individual variation preferences in habitat are also visible in the results of the GLMs. A clear signal towards a preference only of fallow land was observed (always compared to winter cereals as the base variable). The category 'trees/bushes adjacent' is also preferred by all individuals, however there is large variation. For millet, pumpkin, sunflower and soy there is a preference by all but one individual. The least favoured categories show a large variation and all of them have at least one individual who prefers that category over winter cereals (Fig. 10). The results of the GLMs for each individual can be found in Appendix 6.

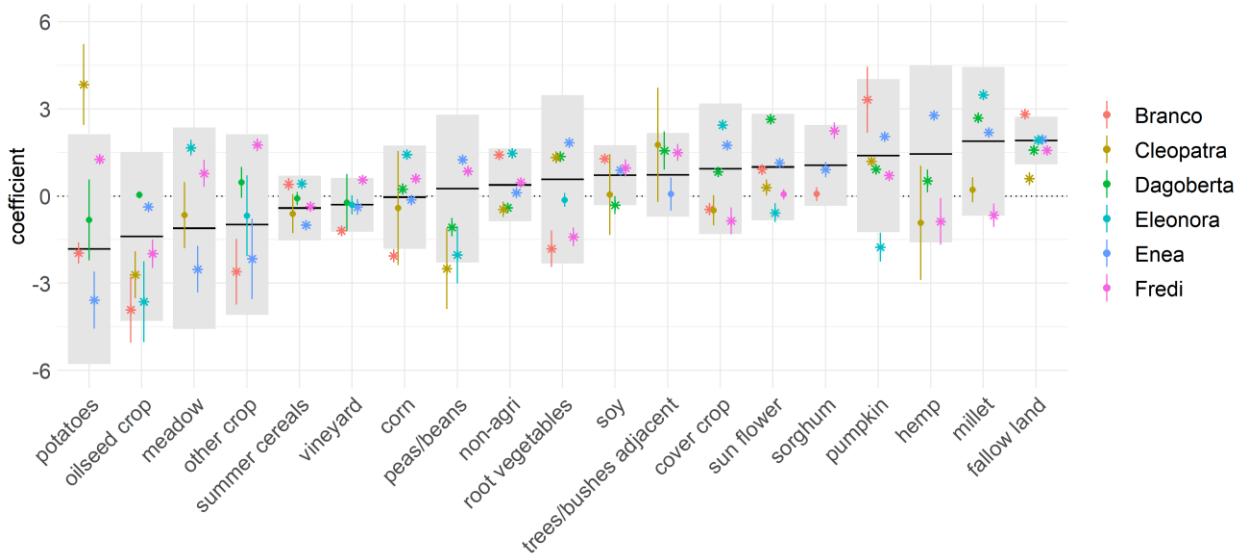

Figure 10: Results of six separate GLMs for each individual with the 'winter cereals' as reference category (intercept). The black lines show the weighted mean and the grey boxes the confidence intervals. Different colours indicate the individuals with whiskers showing the confidence intervals and the stars mark significant results ($p < 0.05$). Categories with a standard error > 10 were excluded as outliers as well as categories with $n < 4$ coefficients.

Discussion

Dispersal

The time frame of the post-fledging dispersal phase fits well those described by Witkowski (1989) in Poland and by Bavoux et al. (1998) in France. Both report large variation in the duration of food provisioning by the parents which is influenced by the age and fitness of the chicks and the quality of the parents (Bustamante & Hiraldo, 1989). The migration start fits perfectly into the pattern reported by Agostini et al. (2017) who observed the migration peak for juveniles between 21st and 25th of September at the Strait of Messina. This distance is covered by Austrian birds within four days (BirdLife Austria, unpublished data). The median departure date for juvenile Marsh Harriers from southern Sweden was exactly the same one as reported here (19th of September; Strandberg et al., 2008), which is surprising given the longer migration of northern breeders but can be explained by large variation in departure dates and relatively small sample sizes. The survival rate of 85 % was between the 70 % (Bavoux et al., 1998) and 95 % (Sternalski et al., 2008) reported from France for the same phase.

Similar to this study, all juvenile Marsh Harriers from southern Sweden made post-independence dispersal movements, some even as far as approx. 400 km (Strandberg et al., 2008). Also Witkowski, (1989) reports large dispersal movements from Poland. However, in a sedentary population in France, all 39 radio-tracked juvenile Marsh Harriers remained in the same salt marsh area they were born, only moving 7 km at most from the nesting site (Sternalski et al., 2008). The same result was confirmed by another study in France where the nest site was still within the

home range after four months (Bavoux et al., 1998). This fits well into the reported pattern that migratory species disperse further than resident ones (Paradis et al., 1998) which holds even true intra-specifically between different populations (Newton, 2010). However, ecologically similar Red Kites (*Milvus milvus*) originating from the same region in Austria, showed further post-independence dispersal movements (Literák et al., 2020), but the species is generally considered more sedentary compared to Marsh Harriers and rarely winters as far as Northern Africa (Literák et al., 2022). The net squared displacement shows a typical picture of dispersal (Bastille-Rousseau et al., 2016) with birds moving long distances to temporary settlement areas in which they only use a relatively small area.

Comparing home range areas is difficult as there is no consensus on the estimation methodology (Laver & Kelly, 2008). Sternalski et al. (2008) report a home range area for the first winter period of 12.5 km² using a different method than this study. Bavoux et al. (1998) report a 29.2 km² home range calculated with Minimum Convex Polygons (MCP) at an age of four months. Both reported home range estimations are much smaller than the 51.9 km² ha (95 % UD) of this study calculated with the dBBMM model, which usually results in smaller home ranges than Kernel Density Estimations (KDE) or MCPs (McGrady et al., 2021). Cardador et al. (2009) report a large variation in the home range sizes calculated with Fixed-Kernel estimates of resident adult Marsh Harriers in Spain. Using the Fixed Kernel (FK) method, the mean home ranges estimated for males after the breeding season were 34 km² (FK 90 %) and 5.6 km² (FK 50 %) (Cardador et al., 2009). Compared to this study, the 90 % value is lower (42.3 km²), but the 50 % value is higher (3.9 km²). This could be interpreted as exploration flights are rarer in experienced adults, but hunting is taking place over a larger area (due to lower prey densities?). However, one must be very cautious with comparing home ranges calculated with different methods.

There was some degree of overlap in the home ranges of different individuals in this study (Fig. 3). Similar patterns were reported by other studies of juveniles (Bavoux et al., 1998) and adults (Cardador et al., 2012; Gamauf & Preleuthner, 1996) hinting at little intraspecific aggression. The dumbbell-shaped hunting areas of adult Marsh Harriers observed by Gamauf and Preleuthner (1996) could not be confirmed.

As predicted, the home range differed with population with larger home ranges in less natural areas. However, the scale of movement was not anticipated, therefore, this effect cannot be explained by nesting locations. For example, birds from the most natural area (Lake Neusiedl) also dispersed large distances to areas outside of the national park. Most of these birds from this area moved to Hungary and then found apparently very good hunting grounds (‘Beate’ in a single large meadow and ‘Branco’ in a single large plot of fallow land; personal observation). From the spatially close location of Hohenau and Hausbrunn, it is noticeable that birds form Hohenau kept more to the west using extensively managed fields in the March-Thaya floodplains (Fig. 3). However, the sample size for each population was very small (n = 3 and n = 4 respectively) and these results, although significant, should be treated with caution (de Winter, 2013). There was

no detectable difference between the home ranges of male and female juvenile Marsh Harriers. Usually females disperse further in raptors (Serrano, 2018).

Behaviour

There is little new literature published about the daily activity cycles of Marsh Harriers. Four reports document (partly) contradicting results; Gamauf and Preleuthner (1996) report an early morning peak in activity between 6 and 8 AM in Austria in summer and lower peaks at 11 AM to 12 PM and 18 PM (CEST) respectively. A different study in the same area reported fairly constant activity from 5 AM to 4 PM with a steep decline afterwards (Sezemsky, 1983). Glutz von Blotzheim et al. (1989) reported that activity and feeding frequency were lowest in the midday and early afternoon hours. These findings might be explained by different prey items which can vary greatly with season and habitat (Cardador et al., 2012; Gamauf & Preleuthner, 1996). Furthermore, raptors are able to adjust their activity patterns to match that of their prey (Lang et al., 2019).

Witkowski (1989) reports high but relatively constant food delivery rates to the nest from 8 AM to 6 PM which can be seen as a proxy for high activity. Only the latter source supports the findings of this study, and the mentioned time frame fits well with the active flight category (Fig. 8), which is also probably the category which can most easily be observed as birds fly low and conspicuously. Transect counts, such as road counts are a common method to count raptors for population estimates (McClure et al., 2021). But it should be noted that detectability is higher when birds are flying, as especially Harriers often sit on the ground hidden by vegetation. One must take into account that the changing frequency, at which Marsh Harriers fly over the course of the day (Fig. 8 and Appendix 5), can have a great impact on the population estimates. Generally, the detectability of Marsh Harriers is probably overestimated as the time spent on the ground varies between 60 % and 90 % and between 9 AM and 3 PM thermals are readily used to cover large distances, which also impairs detectability.

Contrary to this study's hypothesis, the energy intensive flapping behaviour did not decrease after independence. Unfortunately, no study that had investigated the behaviour changes in the post-fledging dispersal phase was found. However, there are some hints from studies on the fledging-dependency period in other Harrier species. Kitowski (2002) studied Montagu's Harriers (*Circus pygargus*) and states that "the total daily time spent flapping by juveniles did not change with their age" but that the total time spent flying increased exponentially opening "the window of dispersion" (Kenward et al., 1993).

There is little evidence of vertical transmission of hunting skills from the parents to offspring during the fledging-dependency period, as they are not following the adults on their hunting trips (Kitowski, 2009; Bavoux et al., 1998; Beske, 1982 for Northern Harriers (*Circus hudsonicus*)). However Bavoux et al. (1998) noted that juveniles were capable of catching small prey right after fledging. Harriers are usually not social hunters, but there is evidence that juveniles hunt more efficiently with other juveniles and even more so with (unrelated) adults nearby (Kitowski, 2009).

The data of this study can be interpreted in such way as the proportion of 'active flight' category increased in the first 12 days after independency but dropped then to a lower level (Fig. 5b). However, this change is rather marginal. Overall, there is little evidence that birds increase their hunting efficiency after independency and there is large variation of the proportion of time spent in 'active flight'.

The ranging and flight behaviour changed before the onset of migration. The days prior to migration are characterised by little movement and birds spent the time mostly sitting. This is evident for all birds at least 15 days prior to departure (Fig. 5c, Fig. 6c, Fig. 7c).

The dispersal characteristics for each individual showed a lot of variation making it difficult to find underlying reasons for dispersal. Individuals hunting in the temporary settlement area did not leave at the same moment, indicating that the food source had not been fully exploited and other mechanisms prompted some individuals to leave the area. One of the influences which could not be investigated in this study is intra- and interspecific competition (Serrano, 2018) on dispersal behaviour, as well as weather patterns. It is reasonable to assume that good weather conditions with thermal updraft positively influence the decision to initiate long-distance dispersal (Hernández-Pliego et al., 2017).

Habitat use and selection

Most habitat studies of Marsh Harriers focussed on the breeding season (Cardador et al., 2011; Sternalski et al., 2008; Gamauf & Preleuthner, 1996). Preferred habitats in Austria were meadows and fallow land whereas vineyards and corn fields were only hunted in rarely but with a high success rate and only some individuals preferred cereals as hunting areas. Rape seed was only preferred early in the season, later the plant cover was too dense to hunt in. Harvest fields were only attractive for a short period (Gamauf & Preleuthner, 1996). In this study, the preference for fallow land was confirmed, whereas meadows were avoided, at least by some individuals. On the other hand, the individual with smallest 50 % UD ('Beate') used a single large meadow in Hungary for most of the post-fledgling dispersal period (personal observation). Thus, at least some meadows seem to be excellent habitat. Vineyards did not show a difference to the reference category. Rape seed fields (summed in 'oilseed crop') were avoided as noted by Gamauf and Preleuthner (1996). In a sedentary Marsh Harrier population in Portugal, saltmarshes and rice fields were selected and corn fields were avoided (Alves et al., 2014). Corn fields were also avoided in the breeding season in Austria (Gamauf & Preleuthner, 1996). However, the results of this study could not confirm this picture as corn fields were not avoided nor selected. Witkowski (1989) noted that juvenile Marsh Harriers dispersed to more productive agricultural areas with a higher rodent abundance and high agricultural intensification led to higher proportion of small mammals in Marsh Harrier diets (Cardador et al., 2012). One factor, which has not been investigated in this study, was the influence of direct human disturbance on the habitat choice. Cardador et al. (2012) found a negative influence of roads on Marsh Harrier abundance.

To summarise, juvenile Marsh Harriers seem to cope well with intensified farmland but nevertheless prefer fallow land within the matrix. This type of land is in the focus of agri-environmental schemes (e.g. the Common Agricultural Policy (CAP) in the EU) to enrich biodiversity which has been under dramatic pressure in Europe (Dudley & Alexander, 2017; Teufelbauer et al., 2017). Hence, increasing biodiversity rich areas, such as fallow land in agricultural areas, also benefits top predators such as Marsh Harriers.

Conclusion

The results of this GPS- and acceleration-informed study demonstrated that juvenile Western Marsh Harriers show large variation in their post-fledging behaviour. They dispersed up to a distance of 167 km from the nest, but when they found suitable hunting areas their 50 % Utility Distribution (calculated with a dBBMM) was relatively small. 15 days before the onset migration they halted their wide-ranging dispersal and stayed at their temporary settlement areas. Through the combination of video footage from the field and tri-axial measurements, a model was built to predict four distinct behaviour classes. The results of this model showed changing proportions of different behaviour classes in the daily activity cycle, with highest mean proportions (40 %) of flight behaviours recorded between 1 PM and 2 PM (CEST). These activity cycles should be considered when interpreting transect counts of raptor species. Contrary to this study's prediction the energy intensive active flight behaviours of juvenile Marsh Harriers did not decrease after independence from the parents indicating that their hunting skills were already sufficiently developed. Despite natural areas in proximity, they moved to agricultural areas and 87 % of recorded locations fell into this habitat. The most commonly available fields were 'winter cereal' crops which were already harvested by the start of the post-fledging dispersal, but Marsh Harriers showed little selection for it. The highest preference was shown for fallow land, which indicates a bottom-up effect in these biodiversity rich areas to top predators, such as the Marsh Harriers. However, for other crop categories there was large individual variation.

Coming back to the movement ecology paradigm (Nathan et al., 2008) this study I attempts to answered the questions how, where and when dispersing juvenile Marsh Harriers move. Nevertheless, the why question, or the underlying mechanism of dispersal respectively, remains the most difficult to answer. Disentangling individual variation and external environmental factors remain a challenge for future studies.

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Supporting Materials

Appendix 1

Table 1 (App.): Overview over the obtained video footage.

birdname	duration (minutes)	observed behaviours
Beate	9	active flight, sitting
Branco	35	active flight, passive flight, sitting
Cleopatra	23	active flight, passive flight, sitting
Dagoberta	17	active flight, passive flight, sitting
Dorian	35	active flight, passive flight, sitting, preening, walking
Eleonore	13	active flight, passive flight, sitting, preening
Enea	23	active flight, passive flight
Fredi	6	active flight, passive flight, sitting
Gustav	9	active flight

Appendix 2

Table 2 (App.): Settings of submodels in FireSOM of Firetail. F = False, T = True.

variable	name of submodel															
	a1	b1	b3	b4	b5	c1	c4	c6	c7	d4	d5	d6	d7	d8	d9	e3
height	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
width	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
use-axis-distribution-x	F	F	T	T	F	F	F	F	F	F	F	T	F	F	F	T
use-axis-distribution-y	F	T	F	F	T	F	T	T	F	T	T	T	T	T	F	F
use-axis-distribution-z	F	T	F	F	F	F	T	F	T	F	T	T	F	F	F	F
use-continuity	T	T	F	F	F	T	F	F	F	F	F	T	F	T	T	T
use-log2-ratio-distribution-xy	F	T	F	T	F	F	F	F	F	F	T	T	F	F	T	F
use-log2-ratio-distribution-xz	F	T	F	T	F	F	F	F	F	T	T	T	F	F	T	F
use-log2-ratio-distribution-yz	F	F	T	F	F	F	F	F	F	F	F	T	F	F	F	F
use-odba	T	T	F	F	F	T	F	F	F	F	F	F	F	F	T	F
use-xyz-vector-norm-distribution	F	T	T	F	T	F	T	F	T	F	T	F	F	T	F	T

Appendix 3

Table 3 (App.): Organisation of submodels and corresponding behaviour classes.

name of submodel					behaviour
a	b	c	d	e	
a1-0,0					active flight
a1-0,1	b1-0,0				inactive ground
	b1-0,1				inactive flight
	b1-1,0				inactive ground
	b1-1,1	c1-0,0	d5-0,0		inactive ground
			d5-0,1		active ground
			d5-1,0		inactive ground
			d5-1,1		inactive flight
		c1-0,1			inactive flight
		c1-1,1			inactive flight
a1-1,0					active flight
a1-1,1	b3-0,0				active ground
	b3-0,1				active flight
	b3-1,0	c4-0,0			active ground
		c4-0,1			active flight
		c4-1,0	d4-0,0		inactive flight
			d4-0,1		active flight
			d4-1,0		active flight
			d4-1,1		active flight
		c4-1,1	d6-0,0		active ground
			d6-0,1		inactive flight
			d6-1,0		active ground
			d6-1,1		inactive flight
	b3-1,1				active flight

name of submodel					behaviour
a	b	c	d	e	
a1-2,0	b4-0,0				active flight
	b4-0,1				active flight
	b4-1,0				active flight
	b4-1,1				active flight
a1-2,1	b5-0,0				inactive flight
	b5-0,1	c7-0,0			active flight
		c7-0,1			inactive flight
		c7-1,0			inactive flight
		c7-1,1			inactive flight
	b5-1,0				active ground
	b5-1,1	c6-0,0	d7-0,0		active ground
			d7-0,1		inactive flight
			d7-1,0		active ground
			d7-1,1		inactive flight
		c6-0,1	d9-0,0		active ground
			d9-0,1		inactive ground
			d9-1,0		inactive ground
			d9-1,1		inactive ground
		c6-1,0			active ground
		c6-1,1	d8-0,0		active ground
			d8-0,1		active ground
			d8-1,0		inactive flight
			d8-1,1	e3-0,0	inactive fligth
				e3-0,1	inactive flight
				e3-1,0	inactive flight
				e3-1,1	inactive fligth

Appendix 4

Table 4 (App.): Original INVEKOS category names and the summarized habitat categories used in this study.

habitat category	INVEKOS category
bioenergy grass	ELEFANTENGRAS (CHINASCHILF, MISCANTHUS SINENSIS)
buckwheat	BUCHWEIZEN
chestnut	EDELKASTANIEN
peas/beans	KICHERERBSEN
corn	SAATMAISVERMEHRUNG
corn	KÖRNERMAIS
corn	ZUCKERMAIS
corn	SILOMAIS
cover crop	PHACELIA
cover crop	LUZERNE
cover crop	KLEE
cover crop	KLEEGRAS
oilseed crop	LEINDOTTER

habitat category	INVEKOS category
cover crop	SONSTIGES FELDFUTTER
cover crop	WINTERWICKEN
cover crop	GRÜNSCHNITTROGGEN / SUDANGRAS
fallow land	GRÜNBRACHE
fallow land	GRÜNLANDBRACHE
fallow land	BIENENTRACHTBRACHE
fallow land	20 JÄHRIGE STILLLEGUNG
fruit	ANDERES OBST
fruit	MARILLEN
fruit	HOLUNDER
fruit	MEHRJÄHRIGE BAUMSCHULEN
fruit	TAFELÄPFEL
fruit	ZWETSCHKEN
fruit	NEKTARINEN
fruit	TAFELBIRNEN
fruit meadow	STREUWIESE
hemp	HANF
jerusalem artichoke	TOPINAMBUR
lentils	LINSEN
oilseed crop	ÖLLEIN (NICHT ZUR FASERGEWINNUNG)
meadow	WECHSELWIESE (EGART, ACKERWEIDE)
meadow	MÄHWIESE/-WEIDE ZWEI NUTZUNGEN
meadow	FUTTERGRÄSER
meadow	EINMÄHDIGE WIESE
meadow/pasture	MÄHWIESE/-WEIDE DREI UND MEHR NUTZUNGEN
millet	HIRSE
mixed crop	SOMMERHARTWEIZEN (DURUM) / FELDGEMÜSE
mixed crop	GEMÜSE IM FOLIENTUNNEL
mixed crop	ERBSEN - GETREIDE GEMENGE
mixed crop	WEIN BODENGESUNDUNG
mixed crop	WINTERGERSTE / BUCHWEIZEN
mixed crop	WICKEN - GETREIDE GEMENGE
mixed crop	ACKERBOHNEN - GETREIDE GEMENGE
mixed crop	WINTERGERSTE / FELDGEMÜSE
mixed crop	GRÜNSCHNITTROGGEN / MAIS
mixed crop	WINTERHARTWEIZEN (DURUM) / FELDGEMÜSE
non-agri	non_agri
nuts	SCHALENFRÜCHTE (WALNÜSSE, HASELNÜSSE, ...)
oilseed crop	SENF
oilseed crop	WINTERMOHN
oilseed crop	SOMMERMOHN
oilseed crop	WINTERRAPS
oilseed crop	MARIENDISTELN
other crop	SONSTIGE ACKERKULTUREN
other crop	SONSTIGE ACKERFLÄCHEN
other crop	SONSTIGE SPEZIALKULTURFLÄCHEN
pasture	DAUERWEIDE

habitat category	INVEKOS category
pasture	SONSTIGE HUTWEIDEFLÄCHEN
peas/beans	KÖRNERERBSEN
peas/beans	PLATTERBSEN
peas/beans	ACKERBOHNEN (PUFFBOHNEN)
peas/beans	ACKERBOHNEN / ERBSENGEMENGE
peas/beans	PELUSCHKEN
potatoes	SPEISEINDUSTRIEKARTOFFELN
potatoes	FRÜHKARTOFFELN
potatoes	SPEISEKARTOFFELN
potatoes	STÄRKEINDUSTRIEKARTOFFELN
pumpkin	ÖLKÜRBIS
pumpkin	SPEISEKÜRBIS
root vegetables	ÖLRETTICH
sorghum	SORGHUM
soy	SOJABOHNEN
spices/medicinal plants	GEWÜRZFENCHEL
spices/medicinal plants	SOMMERKÜMMEL
spices/medicinal plants	WINTERKÜMMEL
spices/medicinal plants	BLUMEN UND ZIERPFLANZEN
spices/medicinal plants	GEWÜRZPFLANZEN
spices/medicinal plants	HEILPFLANZEN
strawberry	ERDBEEREN
root vegetables	ZUCKERRÜBEN
summer cereals	SOMMERHARTWEIZEN (DURUM)
summer cereals	SOMMERWICKEN
summer cereals	SOMMERGERSTE
summer cereals	SOMMERWEICHWEIZEN
summer cereals	SOMMERHAFER
summer cereals	SOMMERMENGGETREIDE
summer cereals	SOMMERTRITICALE
sun flower	SONNENBLUMEN
trees/bushes adjacent	ERSTAUFFORSTUNG ALT
trees/bushes adjacent	LSE HECKE / UFERGEHÖLZ
trees/bushes adjacent	LSE RAIN / BÖSCHUNG / TROCKENSTEINMAUER
trees/bushes adjacent	LSE FELDGEHÖLZ / BAUM- / GEBÜSCHGRUPPE
trees/bushes adjacent	GLÖZ GRABEN / UFERRANDSTREIFEN
root vegetables	FUTTERRÜBEN (RUNKELRÜBEN, BURGUND KOHLRÜBEN)
vegetables	FELDGEMÜSE EINKULTURIG
vegetables	FELDGEMÜSE MEHRKULTURIG
vegetables	FELDGEMÜSE VERARBEITUNG MEHRKULTURIG
vegetables	FELDGEMÜSE VERARBEITUNG EINKULTURIG
vegetables	FELDGEMÜSE FRISCHMARKT UND VERARBEITUNG MEHRKULTURIG
vineyard	WEIN
vineyard	REBSCHULEN
vineyard	SONSTIGE WEINFLÄCHEN
winter cereals	WINTERWEICHWEIZEN
winter cereals	WINTERGERSTE

habitat category	INVEKOS category
winter cereals	WINTERROGGEN
winter cereals	WINTERHARTWEIZEN (DURUM)
winter cereals	WINTERTRITICALE
winter cereals	WINTERHAFER
winter cereals	EMMER ODER EINKORN (WINTERUNG)
winter cereals	WINTERDINKEL (SPELZ)

Appendix 5

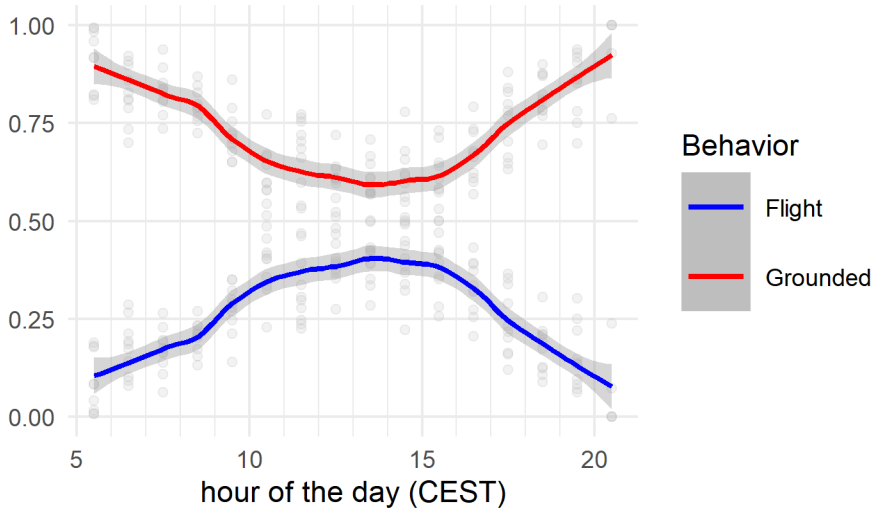

Figure 1 (App.): Average proportion of flight categories (active and passive) and grounded categories (active and passive) in the daily activity cycle.

Appendix 6

Table 5 (App.): Results of the Generalized Linear Models for each individual and mean values.

id	term	coefficient	standard error	z-value	p-value
Branco	(Intercept)	-12.52	0.04	-353.56	0.00
Branco	corn	-2.06	0.12	-17.64	0.00
Branco	cover crop	-0.45	0.11	-4.12	0.00
Branco	fallow land	2.82	0.05	56.64	0.00
Branco	hemp	-12.38	116.58	-0.11	0.92
Branco	lentils	6.66	0.14	48.53	0.00
Branco	meadow	-12.38	48.05	-0.26	0.80
Branco	millet	-12.38	221.57	-0.06	0.96
Branco	mixed crop	-12.38	50.61	-0.25	0.81
Branco	non-agri	1.42	0.04	33.61	0.00
Branco	oilseed crop	-3.91	0.58	-6.76	0.00
Branco	other crop	-2.60	0.58	-4.50	0.00
Branco	peas/beans	-12.38	215.08	-0.06	0.95
Branco	potatoes	-1.96	0.19	-10.54	0.00
Branco	pumpkin	3.31	0.58	5.73	0.00
Branco	root vegetables	-1.82	0.32	-5.70	0.00
Branco	sorghum	0.07	0.12	0.57	0.57

id	term	coefficient	standard error	z-value	p-value
Branco	soy	1.29	0.06	20.97	0.00
Branco	summer cereals	0.41	0.11	3.82	0.00
Branco	sun flower	0.92	0.06	16.43	0.00
Branco	trees/bushes adjacent	-12.38	160.83	-0.08	0.94
Branco	vegetables	0.27	0.06	5.03	0.00
Branco	vineyard	-1.19	0.08	-14.16	0.00
Dagoberta	(Intercept)	-12.88	0.02	-533.03	0.00
Dagoberta	bioenergy grass	-10.02	190.19	-0.05	0.96
Dagoberta	corn	0.24	0.10	2.41	0.02
Dagoberta	cover crop	0.84	0.08	9.93	0.00
Dagoberta	fallow land	1.58	0.04	40.34	0.00
Dagoberta	hemp	0.52	0.20	2.59	0.01
Dagoberta	meadow	-10.02	37.62	-0.27	0.79
Dagoberta	millet	2.69	0.05	52.73	0.00
Dagoberta	non-agri	-0.40	0.06	-6.90	0.00
Dagoberta	oilseed crop	0.04	0.06	0.68	0.50
Dagoberta	other crop	0.47	0.27	1.75	0.08
Dagoberta	peas/beans	-1.07	0.16	-6.70	0.00
Dagoberta	potatoes	-0.82	0.71	-1.16	0.25
Dagoberta	pumpkin	0.92	0.04	21.25	0.00
Dagoberta	root vegetables	1.36	0.05	25.03	0.00
Dagoberta	soy	-0.31	0.16	-2.00	0.05
Dagoberta	summer cereals	-0.08	0.12	-0.72	0.47
Dagoberta	sun flower	2.65	0.03	78.91	0.00
Dagoberta	trees/bushes adjacent	1.57	0.33	4.68	0.00
Dagoberta	vegetables	27.45	333.65	0.08	0.93
Dagoberta	vineyard	-0.23	0.50	-0.46	0.65
Cleopatra	(Intercept)	-12.35	0.06	-214.69	0.00
Cleopatra	corn	-0.41	1.00	-0.41	0.68
Cleopatra	cover crop	-0.49	0.27	-1.85	0.07
Cleopatra	fallow land	0.60	0.12	5.22	0.00
Cleopatra	hemp	-0.92	1.00	-0.92	0.36
Cleopatra	meadow	-0.66	0.58	-1.13	0.26
Cleopatra	millet	0.21	0.22	0.97	0.33
Cleopatra	non-agri	-0.46	0.14	-3.38	0.00
Cleopatra	oilseed crop	-2.71	0.41	-6.56	0.00
Cleopatra	peas/beans	-2.50	0.71	-3.52	0.00
Cleopatra	potatoes	3.84	0.71	5.41	0.00
Cleopatra	pumpkin	1.20	0.09	12.86	0.00
Cleopatra	root vegetables	1.33	0.11	12.57	0.00
Cleopatra	soy	0.05	0.71	0.08	0.94
Cleopatra	summer cereals	-0.61	0.34	-1.79	0.07
Cleopatra	sun flower	0.29	0.14	2.08	0.04
Cleopatra	trees/bushes adjacent	1.76	1.00	1.76	0.08
Enea	(Intercept)	-12.92	0.02	-737.55	0.00
Enea	bioenergy grass	-11.99	156.67	-0.08	0.94
Enea	buckwheat	-11.99	147.88	-0.08	0.94
Enea	chestnut	-11.99	775.49	-0.02	0.99
Enea	corn	-0.13	0.04	-3.49	0.00

id	term	coefficient	standard error	z-value	p-value
Enea	cover crop	1.75	0.04	43.97	0.00
Enea	fallow land	1.95	0.03	77.73	0.00
Enea	fruit	-11.99	56.19	-0.21	0.83
Enea	fruit meadow	-11.99	414.52	-0.03	0.98
Enea	hemp	2.78	0.07	39.02	0.00
Enea	jerusalem artichoke	-11.99	1096.70	-0.01	0.99
Enea	lentils	2.34	0.21	11.43	0.00
Enea	meadow	-2.52	0.41	-6.16	0.00
Enea	meadow/pasture	-11.99	365.57	-0.03	0.97
Enea	millet	2.19	0.05	47.92	0.00
Enea	mixed crop	-11.99	68.15	-0.18	0.86
Enea	non-agri	0.12	0.03	4.27	0.00
Enea	nuts	-11.99	633.18	-0.02	0.99
Enea	oilseed crop	-0.37	0.08	-4.91	0.00
Enea	other crop	-2.16	0.71	-3.06	0.00
Enea	pasture	-11.99	118.95	-0.10	0.92
Enea	peas/beans	1.25	0.06	22.28	0.00
Enea	potatoes	-3.58	0.50	-7.16	0.00
Enea	pumpkin	2.04	0.03	79.79	0.00
Enea	root vegetables	1.84	0.02	75.06	0.00
Enea	sorghum	0.91	0.14	6.63	0.00
Enea	soy	0.89	0.06	15.87	0.00
Enea	spices/medicinal plants	0.63	0.41	1.55	0.12
Enea	strawberry	-11.99	81.74	-0.15	0.88
Enea	summer cereals	-1.00	0.08	-12.50	0.00
Enea	sun flower	1.14	0.05	25.01	0.00
Enea	trees/bushes adjacent	0.07	0.29	0.24	0.81
Enea	vegetables	-11.99	35.20	-0.34	0.73
Enea	vineyard	-0.38	0.14	-2.74	0.01
Fredi	(Intercept)	-12.66	0.03	-496.81	0.00
Fredi	buckwheat	1.05	0.23	4.67	0.00
Fredi	corn	0.60	0.05	13.28	0.00
Fredi	cover crop	-0.86	0.24	-3.60	0.00
Fredi	fallow land	1.57	0.04	41.68	0.00
Fredi	fruit	1.33	0.18	7.21	0.00
Fredi	fruit meadow	-10.24	403.46	-0.03	0.98
Fredi	hemp	-0.87	0.41	-2.13	0.03
Fredi	lentils	-10.24	55.95	-0.18	0.86
Fredi	meadow	0.78	0.24	3.29	0.00
Fredi	millet	-0.66	0.21	-3.22	0.00
Fredi	mixed crop	-0.20	0.32	-0.63	0.53
Fredi	non-agri	0.47	0.04	11.96	0.00
Fredi	nuts	2.08	0.12	17.94	0.00
Fredi	oilseed crop	-1.98	0.25	-7.89	0.00
Fredi	other crop	1.76	0.11	15.53	0.00
Fredi	pasture	-10.24	107.83	-0.10	0.92
Fredi	peas/beans	0.86	0.10	8.95	0.00
Fredi	potatoes	1.27	0.09	13.69	0.00
Fredi	pumpkin	0.71	0.05	13.05	0.00

id	term	coefficient	standard error	z-value	p-value
Fredi	root vegetables	-1.41	0.16	-8.56	0.00
Fredi	sorghum	2.25	0.14	15.66	0.00
Fredi	soy	0.97	0.15	6.31	0.00
Fredi	spices/medicinal plants	3.53	0.09	37.85	0.00
Fredi	summer cereals	-0.36	0.09	-4.13	0.00
Fredi	sun flower	0.07	0.09	0.73	0.47
Fredi	trees/bushes adjacent	1.50	0.15	10.01	0.00
Fredi	vegetables	-10.24	68.20	-0.15	0.88
Fredi	vineyard	0.56	0.04	12.78	0.00
Eleonora	(Intercept)	-13.17	0.04	-351.28	0.00
Eleonora	bioenergy grass	-11.74	775.49	-0.02	0.99
Eleonora	buckwheat	1.76	0.71	2.48	0.01
Eleonora	corn	1.43	0.06	22.81	0.00
Eleonora	cover crop	2.45	0.06	41.73	0.00
Eleonora	fallow land	1.93	0.05	40.14	0.00
Eleonora	fruit	-11.74	365.57	-0.03	0.97
Eleonora	hemp	-11.74	88.09	-0.13	0.89
Eleonora	lentils	-11.74	203.65	-0.06	0.95
Eleonora	meadow	1.66	0.14	11.98	0.00
Eleonora	millet	3.49	0.05	65.43	0.00
Eleonora	mixed crop	-11.74	62.09	-0.19	0.85
Eleonora	non-agri	1.47	0.05	29.23	0.00
Eleonora	nuts	-11.74	233.82	-0.05	0.96
Eleonora	oilseed crop	-3.63	0.71	-5.13	0.00
Eleonora	other crop	-0.68	0.71	-0.96	0.34
Eleonora	peas/beans	-2.02	0.50	-4.04	0.00
Eleonora	potatoes	-11.74	346.81	-0.03	0.97
Eleonora	pumpkin	-1.76	0.25	-6.97	0.00
Eleonora	root vegetables	-0.14	0.12	-1.13	0.26
Eleonora	soy	-11.74	98.49	-0.12	0.91
Eleonora	spices/medicinal plants	-11.74	129.25	-0.09	0.93
Eleonora	summer cereals	0.43	0.08	5.12	0.00
Eleonora	sun flower	-0.58	0.17	-3.46	0.00
Eleonora	trees/bushes adjacent	-11.74	132.03	-0.09	0.93
Eleonora	vegetables	-11.74	447.73	-0.03	0.98
Eleonora	vineyard	-0.30	0.17	-1.82	0.07
Mean	(Intercept)	-12.84	0.19		
Mean	buckwheat	1.34	0.35		
Mean	corn	-0.04	0.91		
Mean	cover crop	0.94	1.15		
Mean	fallow land	1.91	0.42		
Mean	fruit	1.33	0.00		
Mean	hemp	1.45	1.55		
Mean	lentils	3.33	1.81		
Mean	meadow	-1.11	1.77		
Mean	millet	1.89	1.31		
Mean	mixed crop	-0.20	0.00		
Mean	non-agri	0.38	0.64		
Mean	nuts	2.08	0.00		

id	term	coefficient	standard error	z-value	p-value
Mean	oilseed crop	-1.39	1.49		
Mean	other crop	-0.98	1.59		
Mean	peas/beans	0.26	1.30		
Mean	potatoes	-1.82	2.02		
Mean	pumpkin	1.39	1.34		
Mean	root vegetables	0.57	1.48		
Mean	sorghum	1.06	0.71		
Mean	soy	0.72	0.53		
Mean	spices/medicinal plants	1.41	1.29		
Mean	summer cereals	-0.41	0.57		
Mean	sun flower	1.00	0.93		
Mean	trees/bushes adjacent	0.73	0.74		
Mean	vegetables	0.27	0.00		
Mean	vineyard	-0.30	0.47		