



vogelwarte.ch

Swiss Ornithological Institute



University of Natural Resources
and Life Sciences, Vienna

The effect of food supplementation on range use of breeding red kites (*Milvus milvus*) in Switzerland



Master Thesis

for obtaining the academic degree Master of Science
in Wildlife Ecology and Wildlife Management

Eingereicht von: Carl BAUCKS

Matrikelnummer: 01541641

Betreuer:

Univ. Prof. Dr. Lukas Jenni

Swiss Ornithological Institute

Department of Evolutionary Biology and Environmental Studies, University of Zurich

Dr. Martin Gruebler

Swiss Ornithological Institute

Vienna, March 2018





**University of Natural Resources
and Life Sciences, Vienna**

Declaration in lieu of oath

I herewith declare in lieu of oath that this thesis has been composed by myself without any inadmissible help and without the use of sources other than those given due reference in the text and listed in the list of references. I further declare that all persons and institutions that have directly or indirectly helped me with the preparation of the thesis have been acknowledged and that this thesis has not been submitted, wholly or substantially, as an examination document at any other institution.

20.03.2018

Date

Signature

Imprint

Keywords: home range, red kite (*Milvus milvus*), supplementary feeding, Switzerland, GPS telemetry

Citation: Baucks, C (2018). The effect of food supplementation on range use of red kites (*Milvus milvus*) in Switzerland. Master Thesis. University of Natural Resources and Life Sciences, Vienna (BOKU), Department for Integrative Biology and Biodiversity Research, Institute of Wildlife Biology and Game Management (IWJ), Vienna, Austria.

Institutions

University of Natural Resources and Life Sciences, Vienna (BOKU)
Department for Integrative Biology and Biodiversity Research
Institute of Wildlife Biology and Game Management (IWJ)
Gregor-Mendel Strasse 33
A-1180 Vienna

Swiss Ornithological Institute
Seerose 1
CH-6204 Sempach

Abstract (deutsch)

In der Ökologie werden Home-Ranges (HR) benutzt, um die Raumnutzung eines Vogels innerhalb einer meist biologisch bedeutsamen Zeitperiode zu bestimmen. Dieser Ansatz lässt den Einfluss von sich täglich verändernden Umweltfaktoren auf die Raumnutzung von Vögeln im Ungewissen. Von einigen Vögeln ist bereits bekannt, dass sie während der Brutperiode geschlechtsspezifische HR haben. Es bleibt jedoch fraglich, ob dieselben Umweltfaktoren geschlechterspezifische Einflüsse auf die Raumnutzung haben. Um dies zu testen, wurden geschlechterspezifische Auswirkungen von Wettereinflüssen, Nahrungsverfügbarkeiten und Nestlings-Alter auf tägliche HR-Größen quantifiziert. Durch ein Zufütterungs-Experiment, bei dem gezielt Nahrung in Nest-Nähe von GPS-besenderten adulten Rotmilanen während der Nestlings-Aufzucht ausgebracht wurde, konnten Korrelationen zwischen Nahrungsverfügbarkeit und Wetter eliminiert werden. Zur Kontrolle dienten Daten von ungefütterten Individuen. Die Ergebnisse zeigten starke intersexuelle Differenzen in der Raumnutzung, wobei eine Reaktion der Weibchen auf die beschriebenen Variablen ausblieb. Bei Männchen hingegen konnte eine Abnahme der täglichen HR-Größe nachgewiesen werden, wenn Wetterbedingungen ungünstig, die Nahrungsverfügbarkeit hoch war sowie mit fortschreitendem Nestlings-Alter. Die Ergebnisse weisen auf eine effizientere Futtersuche hin, wenn die Nachfrage nach Energie steigt oder punktuell die Nahrungsverfügbarkeit erhöht wird. Die kleineren HR bei ungünstigen Wetterbedingungen deuten jedoch auf einen zu hohen Energieaufwand hin und eine befristete Unterbrechung der Nahrungssuche. Es wurde gezeigt, dass männliche Rotmilane ihre Raumnutzung täglichen Veränderungen ihrer Umwelt anpassen und dass dies wahrscheinlich aus energetischen Gründen passiert. Auf dieser Grundlage ist es möglich, Vorhersagen der Raumnutzung von Rotmilanen der untersuchten Population während der Nestlings-Aufzucht zu treffen.

Abstract (english)

In ecology, home ranges are used to determine a bird's extent of spatial use over a certain, mostly biologically meaningful time-period. This approach keeps effects of daily changing environmental influences in the dark. Of a few raptors it is known, that males have larger home ranges than their females during breeding season. If the same environmental factors reveal sex-specific effects remains in question. Here, I quantified sex-specific effects of different weather influences, food availabilities and nestling ages on the daily home range size. The correlation of food availability and weather was eluded by setting up a nest-selective feeding experiment of GPS-tagged red kites (*Milvus milvus*) during their breeding period. Data from unfed but also breeding individuals was used as control. The results revealed a pronounced sex-specific spatial behavior where females did not change their home range size due to short-term environmental changes. In contrast, males showed decreases of daily home range sizes under adverse weather conditions, on days of feeding and with increasing nestling age. The results point to an increase in foraging efficiency, when energy demand increases, or the food availability is locally raised. However, smaller home ranges under adverse conditions are suggestive of causing too high energy costs and a temporal interruption of foraging. This thesis proofs that male red kites adapt their daily home range behavior to a daily changing environment. This is likely caused by energetic reasons. Based on these results, predictions of range use of red kites in the study area during the nestling period are possible.

Table of contents

1. Introduction	1
2. Material and methods	4
2.1 Background	4
2.2 Study area	4
2.3 Catching and tagging	6
2.4 Feeding	6
2.5 Data origin und preparation	7
2.5.1 Forest area	8
2.5.2 Public feeding	8
2.6 Data analysis	8
3. Results	10
3.1 Minimum number of GPS-fixes for daily home ranges	10
3.2 General description of daily home ranges	12
3.3 Factors affecting size of daily home ranges	13
4. Discussion	20
5. Acknowledgements	24
6. Literature	24
7. Appendix	29

1. Introduction

Home-range is defined as the area an individual uses for its regular activities (Burt 1943). Depending on the relation between benefits of available resources and costs for traveling within the home range and defending it, the size of the home range varies (Caraco 1979). Thus, food-availability plays a fundamental role in determining a bird's home range (Zabel et al. 1995). Campioni et al. (2013) divided influential factors of home range sizes into internal (e.g. health status, sex) and external (e.g. habitat, food) factors. So far, the interactions of external with internal factors determining breeding period home range behavior of bird species and its consequences on home range size have only been established in a few studies (Staggenborg et al. 2017; Kouba et al. 2017). This leads to ambiguity about how and to what extent they affect home ranges. The time-periods for which home ranges were calculated mostly complied to the ecologically meaningful period of its study like years and breeding-seasons (Anderson et al. 2005; Monsarrat et al. 2013; Saïd et al. 2009), but most factors (e.g. reproductive status, food availability, weather) underlie inner-seasonal changes and lead to spatial shifts (López-López et al. 2016). Hence, it becomes apparent that home ranges are always just valid at a certain time-span (Rivrud et al. 2010; Pfeiffer & Meyburg 2015). Although it is crucial for a better understanding of the spatiotemporal dynamics in range use, only very few studies quantified changes in short-term home ranges, in especially daily home ranges, probably because of technical limitations (Caro 2007; Powell 2000). Insights into the use of space per day can give detailed information on preferred environmental conditions (e.g. weather) and reactions to short-term changes, e.g. high food availability in the surrounding of the nest when meadows are mowed. With this information, practical conservation measures can be developed. In birds, the chick-rearing phase is energetically the most demanding period of the biological cycle (Newton 1998). Food limitations are distinct for many altricial species when feeding their young at the nest, thus a central place foraging behavior during this time can be expected, meaning an energy optimizing foraging strategy with recurring to the nest (Santangeli et al. 2012; Newton 1998; Orians & Pearson 1979). With daily home ranges during the nestling period, one can investigate what factors improve or impair parenting performance. To answer population-level questions associated with

these short-term spatiotemporal behaviors one has to sample multiple individuals with a high sample interval over longer time-periods (Powell & Mitchell 2012).

Low food availability, occurring spatially and temporarily, was found to decrease condition, viability, fitness and increase home ranges of birds during breeding season, whereas high food availability decreased it (Frey-Roos et al. 1995; Rosenberg et al. 2003; Perry et al. 2004; Strong & Sherry 2000; González et al. 2006; Liu et al. 2013; Michel et al. 2017). Despite the influences of food availability on these internal factors, only few studies engaged with its impacts on space use (Staggenborg et al. 2017; Michel et al. 2017). Sunde et al. (2014) observed, that distribution and quantity of resources can change between short time-periods due to changing environmental factors (e.g. weather), thus having major effects on range use and time budgets.

Weather has strong influences on an animal's spatial ranging behavior, especially during breeding season (Sunde et al. 2014). In birds, rain, differing windspeeds and temperatures were found to lead to changes in flight activity. Arbeiter et al. (2016) found that at high temperatures the flight activity of European bee-eaters (*Merops apiaster*) is increased, because of their prey activity and Pistorius et al. (2015) discovered short foraging trips under high windspeed conditions and long foraging periods at moderate rainfall events in Cape gannets (*Morus capensis*). In birds of prey, hunting activity and success often get reduced and protection of the offspring is increased under adverse weather conditions (Garcia-Heras et al. 2017; Katzenberger et al. 2015; Kouba et al. 2017; Sergio 2003).

This suggests, that weather conditions and food availability are correlated. Due to this correlation, it can hardly be said what effect these two factors separately have. To disentangle these two effects, it is necessary to work with an experimental approach. In raptors, most studies use large scale feeding stations to understand how populations react to predictable food resources (Monsarrat et al. 2013; Fluhr et al. 2017). To my knowledge, small scale feedings, aiming at supplementing single nests have only been done before by Michel et al. (2017) in little owls (*Athene noctua*). Feeding near the nest can create a spatially and temporary high food availability despite changing weather conditions. Considering the central place foraging theory, a

spatial response in birds can be expected by reducing travel-distances and -duration, resulting in smaller home ranges on days when feeding occurs.

In altricial birds, sexes often have different parenting roles and thus show different behaviors during breeding period. This is likely to influence their range use (Mott et al. 2017; Page et al. 2006; Botha et al. 2017; Ratcliffe et al. 2013; Bassi et al. 2017). Keeley und Bechard (2017) found, that female ferruginous hawks (*Buteo regalis*) spend most of their time at the nest for thermoregulating the chicks and the male has to provide food, but during the growth of chicks, these characteristic behaviors were reduced. Pfeiffer & Meyburg (2015) give evidence for larger home ranges in male red kites (*Milvus milvus*) than female red kites even though intra-seasonal changes are highlighted. It is neither known if sexes adjust their home ranges on a daily base nor if they adapt them to short-term changing weather- and food-conditions differently.

In many raptor species, sex specific home ranges can be expected due to female-biased sexual dimorphism (Miranda et al. 2018). The more pronounced this dimorphism is, the more likely sex-specific prey spectrums are, hence the possibility of differing spatial use increases (e.g. few foraging trips with large prey or many trips with small prey). In red kites, this dimorphism is unincisive. Therefore, a sex specific behavior caused by sexual dimorphism is unlikely.

Pfeiffer & Meyburg (2015) found, that the number of red kite fledglings is negatively correlated with the home range size. In contrast to that, Kouba et al. (2017) found a positive correlation between home range size and number of nestlings in male Tengleman's owls (*Aegolius funereus*). I suggest that in general, larger home ranges can be expected when there are more nestlings because energy demand is higher, thus more food must be brought to the nest, leading to an increased foraging activity likely resulting into larger home ranges.

The aim of this study was to investigate environmental factors affecting sex-specific daily home range sizes and range use. In particular, I experimentally discriminated between the effects of food availability and foraging conditions by supplementary feeding GPS-tagged red kites close to their nests during the chick-rearing period and thus creating an artificial spatiotemporal high food availability despite weather conditions. Therefore, this study primarily will help to better understand the reasons of

spatiotemporal range use of chick-rearing red kite adults, thus giving insights into their energy budgeting through in- or decreasing home range sizes. Furthermore, a determination of influences of advancing chick-rearing period and numbers of nestlings on home range sizes was targeted to compare the results with existing studies, helping to clarify, whether the spatial behavior is population-specific or valid across populations.

2. Material and methods

2.1 Background

Over the last 20 years, red kites expanded their distribution over Switzerland. Numbers estimated in 2009 reveal, that Switzerland had 1200 – 1500 breeding pairs, nowadays making up approximately 10 % of the world's red kite population (Swiss Ornithological Institute 2017). Since the 1990s, the red kite distribution range and population size have continued to grow, leading to an even higher responsibility of Switzerland for this species. This is particularly emphasized, given that red kite populations in most other surrounding countries are either constant or even declining. To explain this exceptionally fast population-growth and -expansion, research settlement and dispersal processes and giving insight into the behavior of Swiss red kites, a large project on red kites was launched in 2015 by the Swiss Ornithological Institute. Diverse methods were applied, including monitoring of territorial birds, catching of red kite adults for ringing and GPS-tagging, food supplementation experiments and climbing of nests for measuring nestlings, ringing and mounting cameras on nest-trees for monitoring purposes.

2.2 Study area

The study area is located predominantly in the Sense-District of canton Fribourg and extends into the districts Saane and See to the west and into canton of Bern to the east (387.5 km²) (Fig. 1). The elevation of the study area reached from 530 m.a.s.l up to 1500 m.a.s.l. 250 - 350 red kites in 2016 with 88 confirmed broods and 400 - 700 in 2017 having 140 confirmed broods inhabited the study area. The landscape is embossed with agriculture. Statistics from 2017 reveal that 45.27 % (756.42 km²) of

the canton is covered by farmland, mainly meadows (67.9 %). The patchy forest-cover claims 25 % (417.7 km²) of the canton's area. The mean land-use per farm was 0.23 km², thus the landscape can be characterized as small-structured. Human population density is 164 citizens per km² (Amt für Statistik StatA 2017).

In addition to red kites, common buzzards (*Buteo buteo*) and black kites (*Milvus migrans*) are the most abundant raptors of the study area.

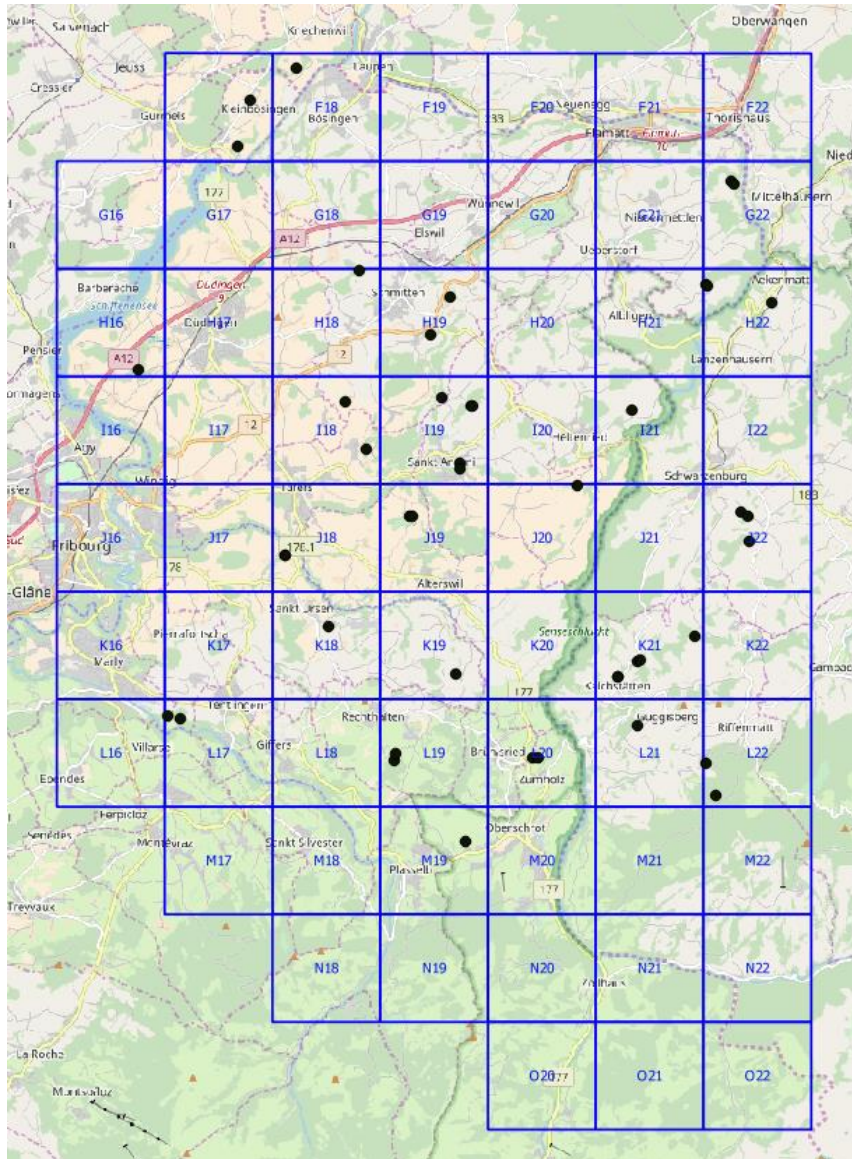


Figure 1: Study area (blue raster) with locations of nests from tagged red kites (black dots) which contribute data to this study. Background map generated with R-package: "leaflet" © OpenStreetMap-contributors.

2.3 Catching and tagging

Catching adults was done during the breeding seasons of 2016 and 2017. A detailed description is given in Sieder (2018). A Dho-gaza net (4 x 6m, 60mm mesh size) was set up close to a red kite nest. A living eagle owl was placed in front of the net to provoke mobbing behavior in the territorial red kites, causing the red kites to get caught in the net whilst they attacked the presented nest predator in pretense. Once an adult was caught, a solar-powered GSM/UHF-GPS-logger (Ecotone, skua-series) was mounted on its back via figure 8 harness (Kenward 2001) with Teflon straps, recording locations approximately every 2 min that were available using UHF-Download and sending hourly positions via GSM. When power levels became low, 2 min sampling stopped first in favor of having continuous hourly GPS-fixes.

2.4 Feeding

Supplementary feeding stations were placed, stratified over an altitude gradient, at active and successful nests of tagged red kites within the study area. Food was provided, at maximum, every second day in 2017. In 2016, the feeding interval was lower, with a maximum of four days between feeding events. For more details on



Figure 2: Red kite swooping at feeding platform. Bottom left: Chicks on platform.

feeding 2016, see Cereghetti (2017). The feeding platforms were made up of a wood-post and a board of 60 x 60 cm on top of it. The height of these platforms ranged around 2 m. The construction, itself, and the locations of the platforms – far enough from higher vegetation (large bushes or trees), in predominantly open areas – prevented mammals from

accessing the top of the platform and thus to feed from it (Fig. 2). Maximum distance from platform to the focus red kite nest was 200 m. For the feeding, dead day-old chicks (mean weight per chick = 38 ± 2.3 g) from a local hatchery were used (Wüthrich Brüterei AG, Belp). To accustom the adults to the platforms, feeding was often started prior to hatching but always after egg laying. According to Orros & Fellowes (2014),

the maximum amount of food a red kite needs per day is 180g (~ 5 day old chicks). Therefore, the minimum number of chicks placed at the platform was 10 to supply the pair for that day with food. As soon as the red kite chicks hatched, another 5 chicks per hatchling were fed for the first 10 days. After these 10 days, 10 chicks were fed per hatchling because their food demand increased. At platforms where I observed other, non-targeted birds feeding, 10 more chicks were fed to lower the effect of food-loss. The food-mass a red kite nestling needs per day is about 150 g (Wasmund 2013; Orros & Fellowes 2014). By providing 10 chicks per nestling every second day, we aimed at ad libitum food for the feeding day. However, as other species were feeding at the platforms, days between feeding days showed no supplementary food with few exceptions. I discriminated 3 experimental groups for the supplementary feeding experiment: unfed individuals, fed individuals at feeding days, and fed individuals at non-feeding days. For the total home range of each individual, I only could discriminate between fed (at minimum once) and unfed individuals.

2.5 Data origin and preparation

The data downloaded from the loggers via Ultra High Frequency (UHF) telemetry were read into R (R Core Team 2017) as csv files. Only data of the nestling period (from first chick hatching to last chick fledging), at least 10 days after starting supplementary feeding the adults, were used. Where hatching and fledging dates were unknown, they were calculated from a growth-curve based on the first (hatching) and last (fledging) wing-length measurement of juveniles (Aebischer 2009). Furthermore, all data of any bird without values for latitude or longitude got removed as well as doubled timestamps. The data then was uploaded to movebank.org, an online database for animal movement data.

I then downloaded the data from movebank.org and read them into R again to have a uniform data format. The number of GPS-fixes per bird and day reached from one to 498 in the time-span of interest from 5:00 until 23:00 with a sampling interval of ~ 2 min. I derived daily weather information from the MeteoSchweiz weather station in Posieux, Fribourg. The sex of each adult was identified at the catching events by controlling for presence of brood patches (females). The number of nestlings was

obtained from protocols of the first nest-climbing event and the nestling age was calculated from the growth-curve of wing-length previously mentioned.

2.5.1 Forest area

I calculated the forest area (km²) in a circular buffer with the radius of the mean home range size surrounding the nest to take into account that the amount of unsuitable foraging habitat, i.e. forests, might affect the home range size (Apdx. 3).

2.5.2 Public feeding

To take public supplementary feeding into account, I calculated the probability of getting fed in the same nest-buffer as the forest area. Therefore, I used the feeding probability map from Cereghetti (2017), where a specific feeding probability was assigned to every raster cell (300 x 300 m). To have a single value for each nest, I merged the probabilities of the raster cells in the buffer circle into a single value. Because there was an almost 100 % chance of getting fed in every nest-buffer, I refrained from taking the feeding probability into account.

2.6 Data-analysis

The “bivnorm”- method with a grid size of 60 x 60 m and a smoothing factor (h) of 100 m was used to calculate daily 95 % fixed kernel density estimators, i.e. daily home ranges for each bird for every day (R-package: “adehabitatHR”, (Calenge 2006)). The same method was used to estimate home ranges over the whole nestling period for every bird by using all the data available in this period. In addition, whole nestling period 95 % minimum convex polygons (MCP) were calculated. Each daily home range was calculated by using the available amount of daily GPS-fixes. Because of great variation in the amounts of GPS-fixes between days and birds due to different power levels of the loggers, it was necessary to evaluate a minimum amount of GPS-fixes to calculate comparable daily home ranges. For this evaluation, I selected only days with more than 90 % (> 448) of the maximum possible daily GPS-fixes to have full daily home ranges. From these days I then generated random subsamples in steps of 50 GPS-fixes (from 50 to 450) and calculated home ranges for each subsample. To

account for variations in the random selection, I did this calculation twice. I set the home range sizes of the subsamples in relation to the bird's daily home range sizes calculated with all GPS-fixes for being able to compare home range sizes amongst days and birds and used this as a home range suitability-index. When the mean indices of two subsamples enclosed the threshold of 95 %, I converged towards this threshold by manually choosing the amount of the GPS-fixes. The final amount of the GPS-fixes then became the minimum amount to calculate daily home ranges from.

I applied a general linear mixed effects model (glmm) with daily home range sizes as response variable and individual ID and nest ID as random factors (R-package: "lme4", (Bates et al. 2015)). As fixed factors, I included the following variables: supplementary feeding (unfed, feeding day and non-feeding day), sex, number of nestlings, age of nestlings, sum of rain per day (mm), mean temperature per day (°C) and mean windspeed (m/s)). When excluding an outlier nest that had more than four times the forest area (1.38 km²) of the mean forest area in a nest buffer $0.32 \text{ km}^2 \pm 0.2$, there was no effect of forest area on home range size, hence the forest area was excluded from the model. Because there was no significant difference between daily home range sizes of unfed individuals and fed individuals at non-feeding days ($p = 0.91$), I continued the analyses with two experimental groups pooling these two groups together and contrasting them to fed individuals at feeding days. In the first evaluation of the effect of brood size, the effect sizes of two and three nestlings were almost equal, but different from one nestling. Thus, in the final model I only discriminated between 1 and more nestlings. Spearman's rank correlation matrix (R-package: "SciViews", (Grosjean 2017)) revealed that no variables were stronger correlated than 0.334 (windspeed and precipitation). As already mentioned, the sexes in many species react different to changing internal and external factors and resource availability is seen as superior factor for home range behavior. Hence, I considered two-way-interactions of all fixed factors with sex and feeding. I applied a step-wise backward selection only of interaction terms using type III anovas (R-package; "car", (Fox & Weisberg 2011)) until only significant interactions remained in the model, but we kept all the main effects in the model regardless of their significance. Results were visualized as effect plots (R-package: "effects", (Fox 2003)).

3. Results

3.1 Minimum number of GPS-fixes for daily home ranges

In total, there were 1427 daily home ranges of 60 breeding attempts of 44 individuals on 53 nests. 90 % of maximum possible daily locations (450 GPS-fixes) were found on 728 days of 51 breeding attempts of 36 individuals on 41 nests. Including 50 randomly selected points per day already accounted for 75.2 ± 22 % of the full home range size. At these 728 days, 260 GPS-points were sufficient to reach an average of 95 ± 9.1 % of the area of the full daily home range size (Fig. 3). I therefore only used days with 260 or more locations per individual to calculate 95 % kernel estimators resulting into 959 daily home ranges of 53 breeding attempts of 37 birds (16 for both years) at 43 nest sites (App. 1).

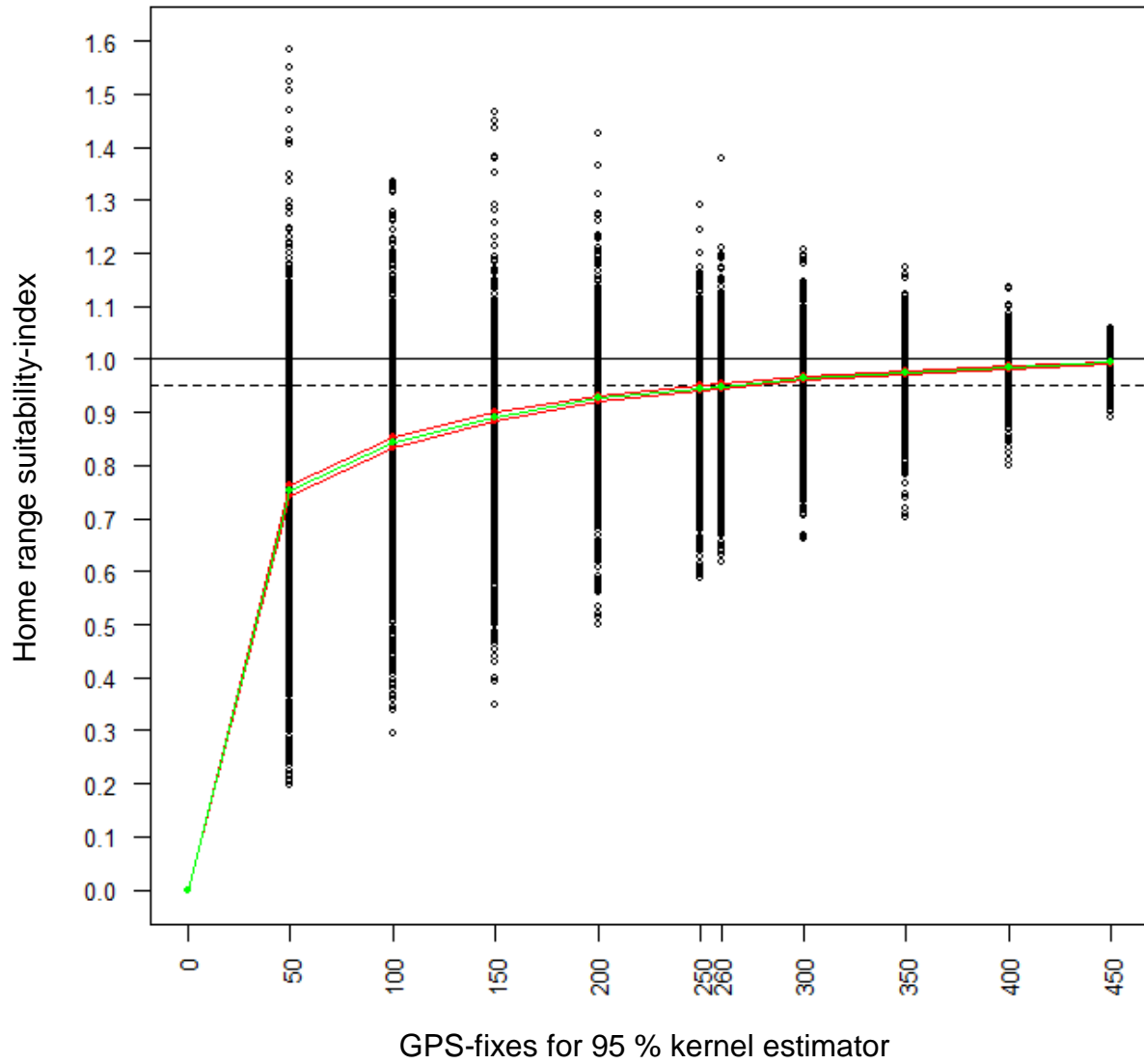


Figure 3: Home range suitability-index at different sample-sizes. continuous black line shows the full breeding attempt home range size; dashed line shows the 95 % threshold; green dots are the mean home range suitability-index of each subsample; within the red dots is the 95 % confidence interval of each subsample.

3.2 General description of daily home ranges

The mean daily home range size was $1.63 \pm 0.79 \text{ km}^2$ and the mean home range size and MPC of a nestling period was $2.78 \pm 3.43 \text{ km}^2$ over all individuals, $5.55 \pm 9.27 \text{ km}^2$ respectively. The final model contained no interactions with feeding but 3 two-way interactions with sex (Tab. 2). Whole-nestling period home ranges were mostly larger than the mean daily home range size (App. 1). Birds used on average $74.6 \pm 18.5 \%$ of their whole-nestling period home range size per day.

In total, I had 18 fed individuals (Tab. 1). 65 feeding days from 7 birds in 2016 and 171 feeding days from 11 birds in 2017 contributed to the general linear mixed model. On average, individuals at feeding days had daily home range sizes of $3.12 \pm 3.17 \text{ km}^2$ ($n = 236$) and unfed ones $3.12 \pm 3.8 \text{ km}^2$ ($n = 723$). Mean daily home ranges on feeding days and whole-nestling period home ranges of fed individuals were slightly larger than on unfed days and unfed individuals respectively, when correcting for sexes (Tab. 1). App. 2 shows an example of daily home ranges of one bird on feeding days and on non-feeding days.

The sex-difference was pronounced with females having mean daily home ranges of $0.87 \pm 0.72 \text{ km}^2$ ($n = 509$) and males $2.5 \pm 2.1 \text{ km}^2$ ($n = 450$, Tab. 1). Furthermore, males' daily use of their whole-nestling period home range size was almost 10 % below females (Tab. 1). At 8 nests both adults contributed data and 4 of these nests were fed. The daily home ranges of these birds also showed that males always had larger daily home ranges than their females despite getting fed or not (App. 1).

338 daily home ranges from 2016 and 621 from 2017 ranging from 21.05. – 06.08.2016 ($\bar{\Delta} 25.06.2016 \pm 14.5$ days) and 01.05. – 15.07.2017 ($\bar{\Delta} 09.06.2017 \pm 14.8$ days) were available. Even though the collected data was from later dates in 2016 than in 2017, sampled days in 2016 showed lower mean temperatures than 2017 (2016: $16.9 \pm 3.7 \text{ }^\circ\text{C}$ 2017: $17.4 \pm 4.7 \text{ }^\circ\text{C}$). They also were rainier compared to the ones from 2017. The mean amount of rain per day was $4.9 \pm 8.6 \text{ mm}$ in 2016 and $2.9 \pm 6.4 \text{ mm}$ in 2017. Mean windspeed per day was $2.1 \pm 1.2 \text{ m/s}$ in 2016 and $2.3 \pm 1.2 \text{ m/s}$ in 2017. There were no differences in means of daily home range sizes under favorable and adverse weather conditions in females but for males, mean daily home ranges

were larger under favorable weather conditions resulting into greater use of whole-nestling period home range sizes (Tab. 1).

On average, there were 1.97 ± 0.66 nestlings per nest. Mean daily home range of red kites with one chick was 1.79 ± 1.93 km² (n = 155), for those with two 1.4 ± 1.62 km² (n = 527) and three 1.99 ± 1.77 km² (n = 277).

Table 1: Mean home range sizes in km² (\pm standard deviation) and sample sizes (N) of the total home ranges over the nestling period (total home range) and the daily home ranges for the two sex, in different supplementary feeding groups and weather conditions (favorable: precipitation = 0 mm and windspeed < 5.5 m/s; adverse: precipitation \geq 5 mm or windspeed \geq 5.5 m/s). Daily use of total home range in percent.

	total home range	N	daily home range	N	% total hr per day
♂ fed	4.6 ± 3	7	2.48 ± 1.34	103	53.9
♂ unfed	4.79 ± 5.27	16	2.51 ± 2.28	347	52.4
♀ fed	1.1 ± 0.5	11	0.7 ± 0.52	133	63.6
♀ unfed	1.53 ± 1.37	19	0.93 ± 0.77	376	60.8
♂ favorable	4.73 ± 4.62	23	2.85 ± 2.36	280	60.3
♂ adverse	4.73 ± 4.62	23	2.51 ± 2.11	99	53.1
♀ favorable	1.38 ± 1.14	30	0.85 ± 0.7	314	61.6
♀ adverse	1.38 ± 1.14	30	0.86 ± 0.72	104	62.3

3.3 Factors affecting size of daily home ranges

Fed red kites had significantly smaller home-ranges than unfed red kites (Tab. 2, Fig. 4) irrespective of their sex. The two-way interaction of feeding and sex was nearly significant, showing a greater effect of feeding in males than females, but was excluded from the model due to the methodological approach.

Temperature had no significant effect on the size of home ranges (App. 4). The interactions with sex showed, that precipitation and windspeed had significant effects on home ranges of males, but not on those of females (Fig. 6, Fig. 7). With increasing windspeed and rain, male red kites reduced their daily home range sizes and approached the home range size of females. In contrast, home ranges of females

remained constant. On days with adverse weather conditions (precipitation ≥ 5 mm or windspeed ≥ 5.5 m/s), the mean daily use of the individual's whole-nestling period home range size was on average only 65.53 ± 36.88 % ($n = 202$) over all individuals, whereas at favorable days (precipitation = 0 mm and windspeed < 5.5 m/s), 72.7 ± 43.6 % ($n = 594$) was used.

With only one chick, red kites had larger daily home ranges than those with 2 or 3 (Fig. 8). When nestlings were young, males had large daily home ranges, but their size was reduced with increasing nestling age. However, male home ranges were still larger at the end of the nesting season compared to female home ranges (Fig. 5). In contrast, females' daily home ranges did not show significant changes over the nestling period.

Table 2: Output of the general linear mixed model investigating factors affecting the size of daily home ranges. Estimates of fixed factors, standard error, lower (2.5 %) and upper (95 %) credibility intervals, X^2 and p-value are given. Significant terms are written in bold.

term	estimate	std.error	t-value	2.5%	97.5%	X^2	p-value
Intercept	0.9809	0.4050	2.4217	0.1724	1.7630	5.8648	0.0154
sexm	3.0956	0.4249	7.2848	2.2574	3.9160	53.0685	0.0000
age	0.0078	0.0049	1.5753	-0.0019	0.0178	2.4814	0.1152
windspeed	-0.0033	0.0487	-0.0681	-0.0994	0.0903	0.0046	0.9457
precipitation	-0.0084	0.0087	-0.9668	-0.0259	0.0085	0.9347	0.3337
nestlings 2 and 3	-0.6589	0.2491	-2.6450	-1.1375	-0.1483	6.9959	0.0082
fedunfed	0.2556	0.1080	2.3678	0.0408	0.4674	5.6064	0.0179
temperature	0.0038	0.0128	0.2986	-0.0213	0.0294	0.0892	0.7652
sexm:age	-0.0307	0.0067	-4.5794	-0.0441	-0.0177	20.9710	0.0000
sexm:windspeed	-0.1716	0.0689	-2.4901	-0.3032	-0.0360	6.2007	0.0128
sexm:precipitation	-0.0453	0.0123	-3.6852	-0.0697	-0.0210	13.5808	0.0002

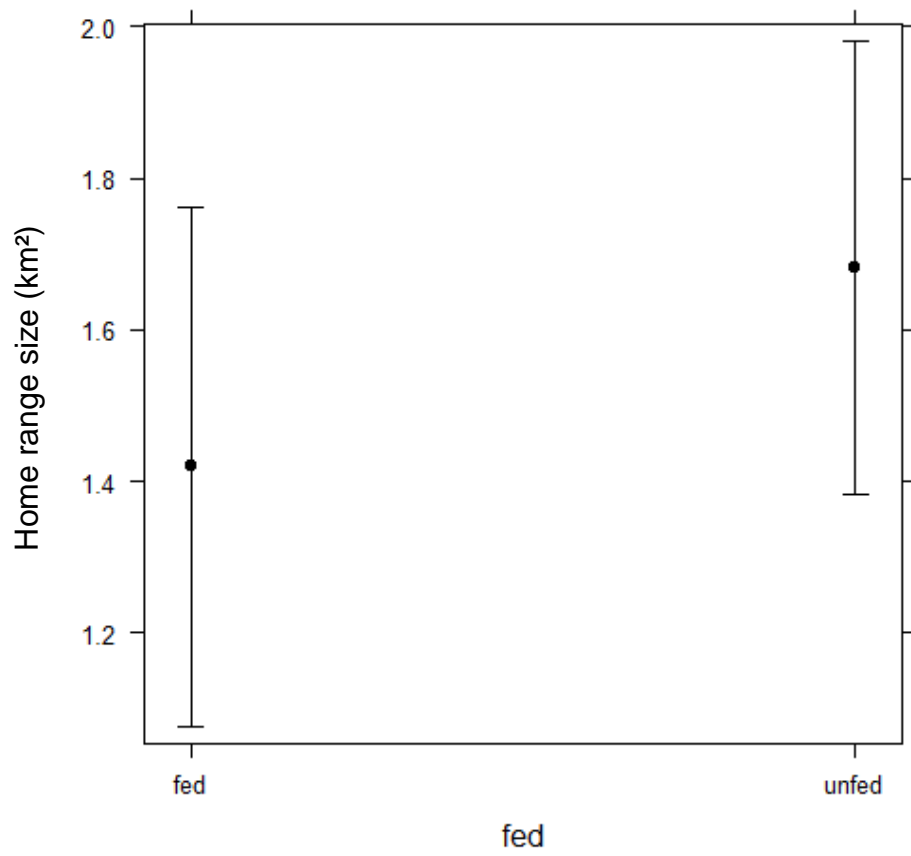


Figure 4: Predicted values for daily home range size for fed and unfed individuals. Error bars represent 95 % confidence intervals.

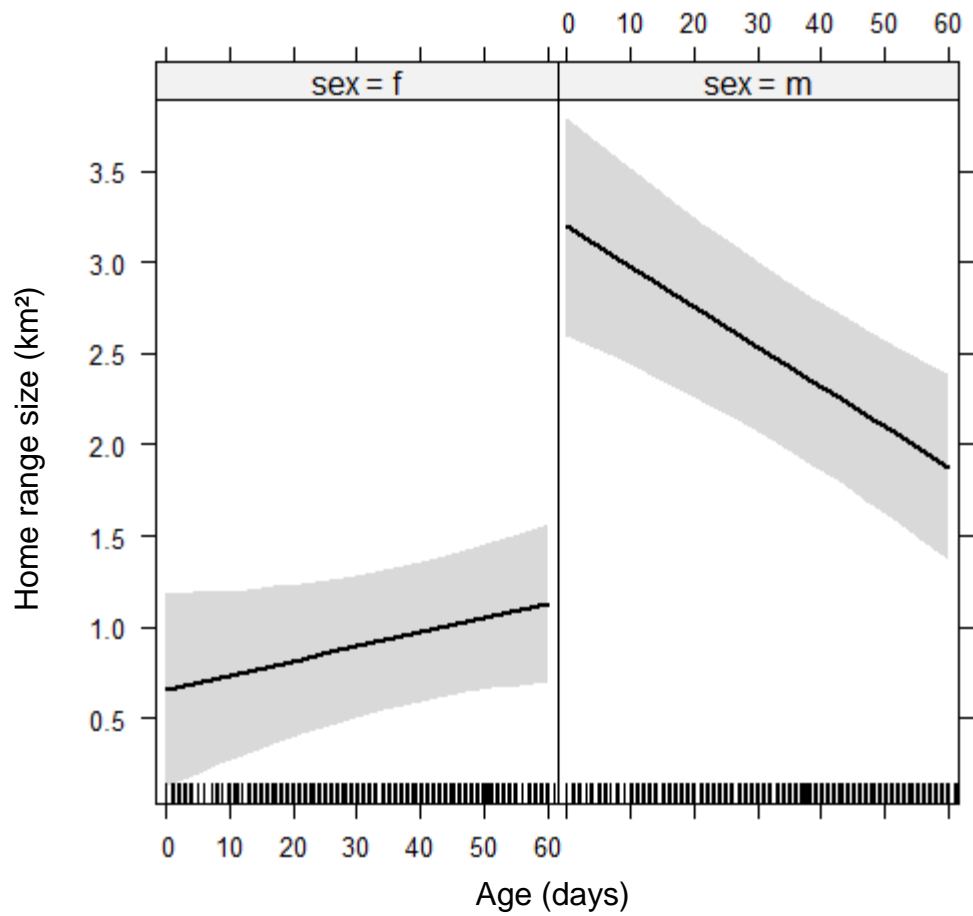


Figure 5: Predicted values of the interaction effect between sex and nestling age (days) on daily home range size. Shaded area represents 95% confidence interval.

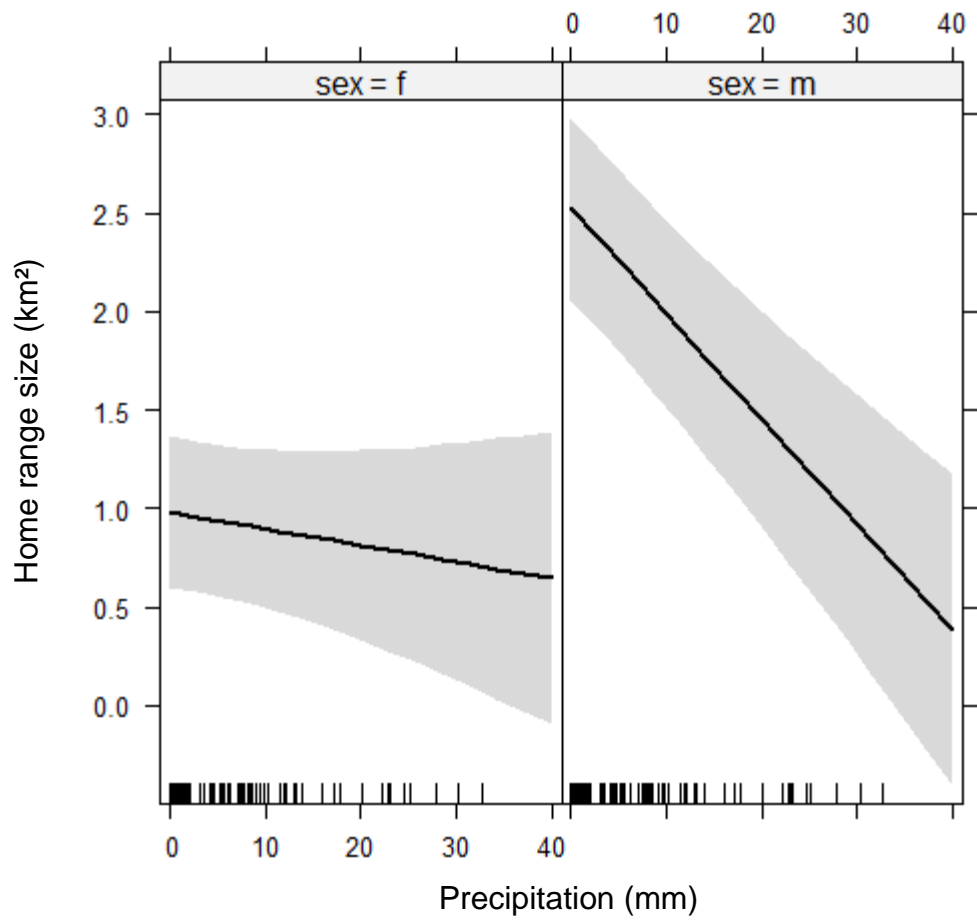


Figure 6: Predicted values of the interaction effect between sex and precipitation (mm per day) on daily home range size. Shaded area represents 95 % confidence interval.

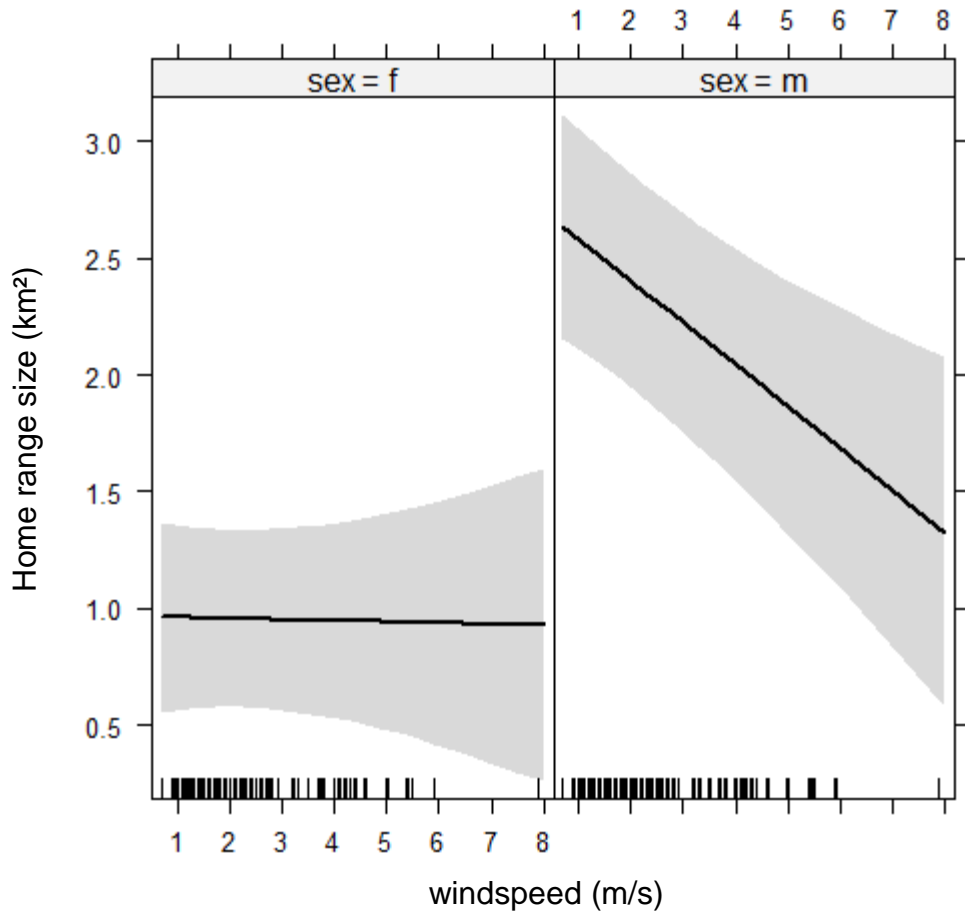


Figure 7: Predicted values of the interaction effect between sex and windspeed (meter per second) on daily home range size. Shaded area represents 95 % confidence interval.

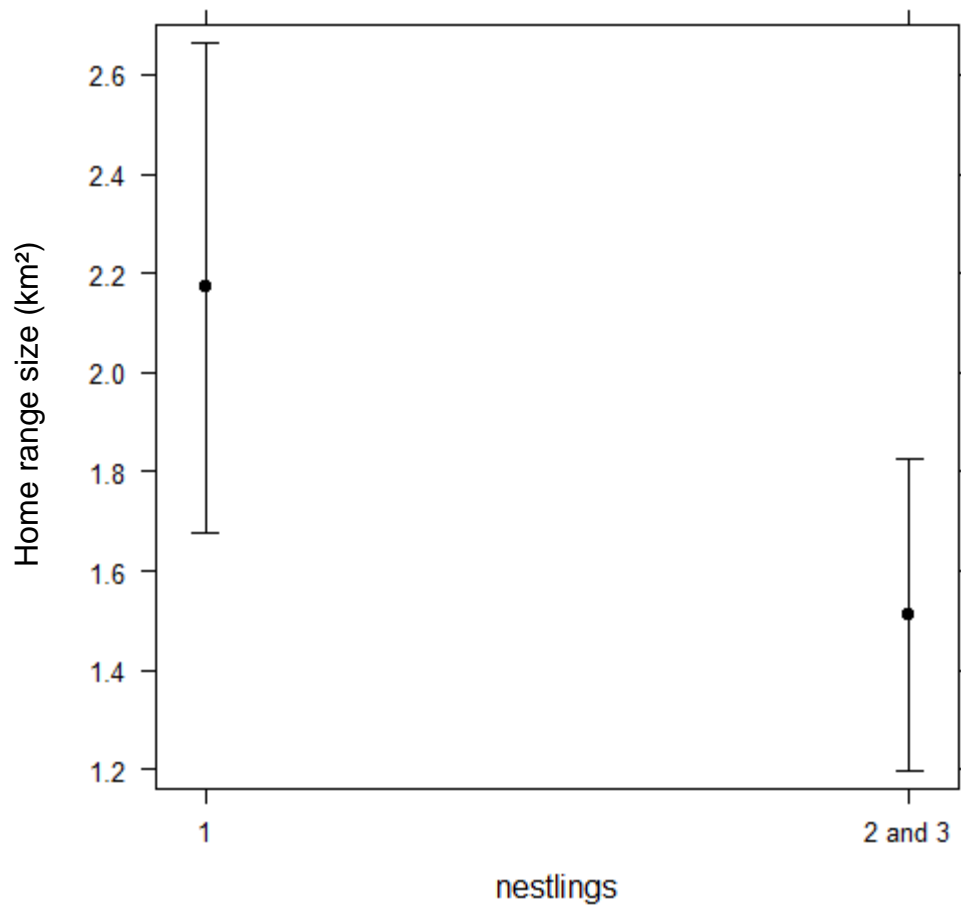


Figure 8: Predicted values of daily home range size for individuals with either one and more nestlings. with Error bars represent 95 % confidence intervals.

4. Discussion

The results of this study showed, that red kites adjusted the size of their daily home range to short-term temporal changes in environment and to the changing needs of their brood. High sample rates of GPS-fixes via modern solar-powered tags made it possible to calculate daily home ranges with unprecedented accuracy. The daily changes in food availability and weather conditions, and the increase in nestling age showed significant effects on the daily home range size of male but not female red kites. The daily home range size was negatively related to number of nestlings. Small daily home ranges in males were associated with adverse weather conditions, high food availability (supplementary feeding) and increasing nestling age and number. This thesis therefore provides strong evidence that factors shaping home ranges in red kites are sex specific and they mainly affect male but not female home range size. For central Germany, Pfeiffer & Meyburg (2015) already detected males having larger breeding season home ranges than females had, but these home ranges were considerably larger compared to the whole-nestling period home ranges in my study area, even though they also used 95 % kernel home ranges and MCPs. During the nestling period, Swiss red kites used less than 2 % of the mean home range size of German red kites when their young were “small” and “large” (Pfeiffer & Meyburg 2015: Tab.3). Even the Swiss red kites’ MCPs were only approximately 10 % of those of German red kites. This difference is rather caused by ecological reasons than methodological reasons. Different smoothing factors (h), grid sizes or sample sizes could have led to differences in results of the 95 % kernel home ranges. However, the difference in MCPs could not. Thus, I suggest, that there are fundamental differences between the study areas, supposedly mainly differences in food availability worth investigating. Because breeding population density was high in the Swiss study area and the probability I found of an anthropogenic food source being present in the buffer of the nest was near 100 % for all of this studies’ nests, I suppose, that in general, the food availability in the study area was higher than in central Germany.

Reversed sexual dimorphism is pronounced in many raptor species and established as an adaptive consequence of the sexual roles (Newton 1998). The difference in size can lead to different prey species, thus temporally and spatially different food

availabilities and foraging strategies (Weimerskirch et al. 2006). Hence, it is likely that home ranges vary in size and orientation for differently sized individuals of the same nest. For this studies' results, the roles of sexes were more likely the reason for intersexual differences, because sex dimorphism in red kites is incisive. Males are predominantly responsible for food supply during chick rearing, thus likely more influenced by the environment whereas females spend most of their time at the nest as long as nestlings rely on her to portion, maintaining thermoregulation and guard them from rain and predators (Aebischer 2009; Newton 1998). When nestlings get able to thermoregulate and later feed by themselves, females can rearrange their time budgets in favor of foraging, but with regard on guarding, they are probably still spatially restricted to the nest area. Current analysis of pictures of nest cameras in the study area suggest, that females still feed their chicks even if they are close to fledging. This would explain the small daily home ranges in females during the whole nesting period.

The strong negative influence of nestling age on home range size for males only is likely the result of the differing roles of sexes, increasing energy demand during nestling growth (Wasmund 2013) and temporally changing food availabilities. Because of the increasing food demand over time, foraging must become more efficient. The predictions of optimal foraging theory assuming the optimization of the net energy intake by decreasing energy costs (e.g. foraging time) or increasing energy intake (e.g. prey quality or quantity) (Mitchell & Powell 2012) may be applied to the results but only when considering central place foraging. This theory assumes, that longer and further foraging trips only occur, if the net energy intake increases (Orians & Pearson 1979). This might be the case, when resources are more available or have a higher quality in more distant places. Here, I suggest an approximately spatial homogenous but temporally increasing food availability due to the reproductive activity of common voles (*Microtus arvalis*) and water voles (*Arvicola terrestris*) (Jenrich et al. 2010). Without an increase of food availability during the nestling period, adults should have consistent home ranges. Thus, when more energy is required, the range use should be reduced towards the nest, but only if the food availability is high enough to cover the demand. This would explain the decreasing home range sizes I found.

The high food availability at a single spot close to the nest, created by supplementary feeding in this study, likely brought benefits to red kites. The closely located high food availability resulted in lower foraging costs in terms of both, time and energy expenditure. First, foraging time, travelling time and – potentially – handling time was shortened by food supplementation. Second, the travelling distance became also shorter resulting in spending more time closer to the nest. Thus, these two advantages were likely the reason for smaller daily home ranges when red kites were fed. Michel et al. (2017) also found a decrease of home range size due to high food availability in little owls (*Athene noctua*). The hypothesis, that males would show a significantly stronger spatial reaction to feedings was not confirmed by my model but there was a strong tendency for it. When calculating daily home range sizes with different amounts of GPS-fixes, the interaction between sex and feeding became significant. Applying a larger sample size would likely show these differences.

Weather-characteristics determine the survival of nestlings, thus fitness of the parents (Kobayashi & Nakamura 2013). Therefore, high effort is put into keeping nestlings warm and dry, in order to maintain their body temperature (Newton 1998). Under adverse weather conditions (rain and strong wind), the danger of losing chicks is raised, making one adult – mostly the female – stay at the nest (Aebischer 2009). During rainfall or strong winds, foraging effort increases and thus energy expenditure, too. When the foraging effort surmounts the hunting success – equal to energy intake –, an energetically disadvantage is the consequence making foraging become unprofitable. Hence, an interruption of foraging and waiting out the shower at a place of minimum energy loss, thus reducing the space use, would be coherent. These two explanations probably were the reasons for birds to restrict their spatial movement as shown in small daily home ranges during adverse weather conditions. Schifferli et al. (2014) found this behavior in Barn swallows (*Hirundo rustica*) and showed, that parents did not relinquish their own energy demands for supplying their chicks under adverse weather conditions. This analog behavior suggests that red kites could behave on the same purpose. Be it that under adverse weather conditions, red kites do behave like barn swallows, longer periods under these conditions would lead to danger of dying nestlings.

Red kites with only one chick used larger areas per day than those who had two or three. This contradicts my hypothesis, that red kites need more space to find sufficient food when having more chicks. This result could be explained by the need of foraging efficiency with more nestlings or/and a result of a different food availability near the nest. The first possibility suggests, that red kites with just one chick didn't need to be efficient when foraging because they have more time available. In contrast, red kites with two or three nestlings probably had to constrain their activity closer to the nest and use their time more efficiently to forage and feed nestlings. This behavior was confirmed by Sieder (2018), who found an earlier detection of potential nest predators in red kites, when there was more than one nestling. Following up the second possibility, food availability near nests, where two or three nestlings are in, is higher than when there is just one nestling, thus travelling further distances would contradict the optimal foraging theory. A negative correlation of fledgling number and home range size was already shown in Pfeiffer & Meyburg (2015) and discussed as result of habitat quality.

The feeding experiment revealed two separate effects. First, under adverse foraging conditions, home ranges became smaller and second, low food availability near the nest resulted into larger home ranges. This strongly points to the need of considering food availability and weather when interpreting home range sizes, because small home ranges could either be a result of high food availability or a consequence of adverse weather conditions, which are two opposing influences. Furthermore, classifying adverse weather conditions as temporal low food availability can lead to heavy misinterpretations.

In conclusion, this study showed, that short-term changes in food availability and weather have strong influences on red kite home range sizes. Consequently, the spatiotemporal range use gets adapted every day due to the prevalent environmental conditions. Based on the results, predictions of range use of red kites in the study area during the nestling period are possible. The high density of red kites in the study area can be explained by the small daily and nestling period home ranges I found. They suggest a high food availability, thus a high habitat quality all over the study area.

Reasons for that are mostly unknown. Further research trying to explain the high density of red kites in the study area should focus on species-habitat relationships.

5. Acknowledgements

I would like to thank Dr. Martin Gruebler for supervising and helping me whenever needed, Prof. Dr. Lukas Jenni for making this thesis possible, Patrick Scherler and Stephanie Witczak for being awesome fieldwork leaders, Julien Fattebert for his statistical support and the whole Red kite project team of 2017 from the Swiss Ornithological Institute for giving me a great time in beautiful Schmitten. A special thanks to my parents for mental and financial support and Daniela Nagl who always listened to any kind of problems I had and sharing the joy over nature.

7. References

Aebischer, A (2009). Der Rotmilan. 1st. Haupt, Bern.

Amt für Statistik StatA (2017). Statistische Jahrbuch des Kantons Freiburg 2018. 47th, Freiburg.

Anderson, DP. ; Forester, JD. ; Turner, MG. ; Frair, JL. ; Merrill, EH. ; Fortin, D. ; Mao, JS. ; Boyce, MS. (2005). Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. *Landscape Ecology*, 20 [3], pp. 257–271. DOI: 10.1007/s10980-005-0062-8.

Arbeiter, S. ; Schulze, M. ; Tamm, P. ; Hahn, S. (2016). Strong cascading effect of weather conditions on prey availability and annual breeding performance in European bee-eaters *Merops apiaster*. *Journal of Ornithology*, 157 [1], pp. 155–163. DOI: 10.1007/s10336-015-1262-x.

Bassi, E. ; Trotti, P. ; Brambilla, M. ; Diana, F. ; Sartirana, F. ; Galli, L. ; Pedrotti, L. (2017). Parental investment in two large raptors breeding in a high prey density area. *Journal of Ornithology*, 158 [2], pp. 549–559. DOI: 10.1007/s10336-016-1407-6.

Bates, D. ; Mächler, M. ; Bolker, B. ; Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67 [1]. DOI: 10.18637/jss.v067.i01.

Botha, JA. ; Rishworth, GM. ; Thiebault, A. ; Green, DB. ; Pistorius, PA. (2017). Sex-specific foraging over space and time in Cape gannets during chick rearing. *Marine Ecology Progress Series*, 579 [], pp. 157–167. DOI: 10.3354/meps12299.

- Burt, WH.** (1943). Territoriality and Home Range Concepts as Applied to Mammals. *Journal of Mammalogy*, 24 [3], pp. 346. DOI: 10.2307/1374834.
- Calenge, C.** (2006). The package adehabitat for the R software. *Ecological Modelling* [197], pp. 516–519.
- Campioni, L. ; del Mar Delgado, M. ; Lourenço, R. ; Bastianelli, G. ; Fernández, N. ; Penteriani, V.** (2013). Individual and spatio-temporal variations in the home range behaviour of a long-lived, territorial species. *Oecologia*, 172 [2], pp. 371–385. DOI: 10.1007/s00442-012-2493-7.
- Caraco, T.** (1979). Time Budgeting and Group Size. *Ecology*, 60 [3], pp. 611–617. DOI: 10.2307/1936081.
- Caro, T.** (2007). Behavior and conservation. *Trends in ecology & evolution*, 22 [8], pp. 394–400. DOI: 10.1016/j.tree.2007.06.003.
- Cereghetti, E** (Feb. 2017). Can supplementary feeding explain the breeding success of the red kite (*Milvus milvus*) in Switzerland?, Zurich.
- Fluhr, J. ; Benhamou, S. ; Riotte-Lambert, L. ; Duriez, O.** (2017). Assessing the risk for an obligate scavenger to be dependent on predictable feeding sources. *Biological Conservation*, 215 [], pp. 92–98. DOI: 10.1016/j.biocon.2017.07.030.
- Fox, J.** (2003). Effect Displays in R for Generalised Linear Models. *Journal of Statistical Software*, 8 [15]. DOI: 10.18637/jss.v008.i15.
- Fox, J. & Weisberg, S** (2011). *An {R} Companion to Applied Regression*. 2nd. Sage, Thousand Oaks, USA.
- Frey-Roos, F. ; Brodmann, PA. ; Reyer, HU.** (1995). Relationships between food resources, foraging patterns, and reproductive success in the water pipit, *Anthus sp. Spinoletta*. *Behavioral Ecology* [6], pp. 287–295.
- Garcia-Heras, MS. ; Mougeot, F. ; Simmons, RE. ; Arroyo, B.** (2017). Regional and temporal variation in diet and provisioning rates suggest weather limits prey availability for an endangered raptor. *IBIS*, 159 [3], pp. 567–579. DOI: 10.1111/ibi.12478.
- González, LM. ; Margalida, A. ; Sánchez, R. ; Oria, J.** (2006). Supplementary feeding as an effective tool for improving breeding success in the Spanish imperial eagle (*Aquila adalberti*). *Biological Conservation*, 129 [4], pp. 477–486. DOI: 10.1016/j.biocon.2005.11.014.
- Graul, C.** (2016). leafletR: Interactive Web-Maps Based on the Leaflet JavaScript Library. R package version 0.4-0. <http://cran.r-project.org/package=leafletR>. 17.03.2018.
- Grosjean, P.** (2017). SciViews-R. <http://www.sciviews.org/SciViews-R>. 17.03.2018.

- Jenrich, J. ; Löhr, PW. ; Müller, F. ; Lang, J** (2010). Kleinsäuger. Imhof, Petersberg.
- Katzenberger, J. ; Tate, G. ; Koeslag, A. ; Amar, A.** (2015). Black Sparrowhawk brooding behaviour in relation to chick age and weather variation in the recently colonised Cape Peninsula, South Africa. *Journal of Ornithology*, 156 [4], pp. 903–913. DOI: 10.1007/s10336-015-1199-0.
- Kenward, R** (2001). A manual for wildlife radio tagging. 2nd. Academic Press, London.
- Kobayashi, A. & Nakamura, H.** (2013). Chick and juvenile survival of Japanese rock ptarmigan *Lagopus muta japonica*. *Wildlife Biology*, 19 [4], pp. 358–367. DOI: 10.2981/13-027.
- Kouba, M. ; Bartoš, L. ; Tomášek, V. ; Popelková, A. ; Šťastný, K. ; Zárbybnická, M.** (2017). Home range size of Tengmalm's owl during breeding in Central Europe is determined by prey abundance. *PloS one*, 12 [5], pp. e0177314. DOI: 10.1371/journal.pone.0177314.
- Liu, Y. ; Webber, S. ; Bowgen, K. ; Schmaltz, L. ; Bradley, K. ; Halvarsson, P. ; Abdelgadir, M. ; Griesser, M.** (2013). Environmental factors influence both abundance and genetic diversity in a widespread bird species. *Ecology and evolution*, 3 [14], pp. 4683–4695. DOI: 10.1002/ece3.856.
- López-López, P. ; de La Puente, J. ; Mellone, U. ; Bermejo, A. ; Urios, V.** (2016). Spatial ecology and habitat use of adult Booted Eagles (*Aquila pennata*) during the breeding season. *Journal of Ornithology*, 157 [4], pp. 981–993. DOI: 10.1007/s10336-016-1357-z.
- Michel, VT. ; Naef-Daenzer, B. ; Keil, H. ; Gruebler, MU.** (2017). Reproductive consequences of farmland heterogeneity in little owls (*Athene noctua*). *Oecologia*, 183 [4], pp. 1019–1029. DOI: 10.1007/s00442-017-3823-6.
- Miranda, EBP. ; Campbell-Thompson, E. ; Muela, A. ; Vargas, FHernán.** (2018). Sex and breeding status affect prey composition of Harpy Eagles *Harpia harpyja*. *Journal of Ornithology*, 159 [1], pp. 141–150. DOI: 10.1007/s10336-017-1482-3.
- Mitchell, MS. & Powell, RA.** (2012). Foraging optimally for home ranges. *Journal of Mammalogy*, 93 [4], pp. 917–928. DOI: 10.1644/11-MAMM-S-157.1.
- Monsarrat, S. ; Benhamou, S. ; Sarrazin, F. ; Bessa-Gomes, C. ; Bouten, W. ; Duriez, O.** (2013). How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers? *PloS one*, 8 [1]. DOI: 10.1371/journal.pone.0053077.
- Mott, R. ; Herrod, A. ; Clarke, RH.** (2017). Resource partitioning between species and sexes in Great Frigatebirds and Lesser Frigatebirds. *The Auk*, 134 [1], pp. 153–167. DOI: 10.1642/AUK-16-184.1.

- Newton, I** (1998). Population limitation in birds. Academic Press, San Diego Calif. u.a.
- Orians, GH. & Pearson, NE** (1979). On the theory of central place foraging, pp. 155–625. In: Analysis of Ecological Systems. Horn, DJ; Mitchell, RD; Stairs, GR. Ohio State University Press. Columbo.
- Orros, ME. & Fellowes, MDE.** (2014). Supplementary feeding of the reintroduced Red Kite *Milvus milvus* in UK gardens. *Bird Study*, 61 [2], pp. 260–263. DOI: 10.1080/00063657.2014.885491.
- Page, B. ; McKenzie, J. ; Sumner, MD. ; Coyne, M. ; Goldsworthy, SD.** (2006). Spatial separation of foraging habitats among New Zealand fur seals. *Marine Ecology Progress Series*, 323 [], pp. 263–279. DOI: 10.3354/meps323263.
- Perry, MZ. ; Beissinger, SR. ; Newman, SH. ; Burkett, EB. ; Williams, TD.** (2004). Applying the Declining Population Paradigm. *Conservation Biology*, 18 [4], pp. 1088–1098. DOI: 10.1111/j.1523-1739.2004.00134.x.
- Pfeiffer, T. & Meyburg, BU.** (2015). GPS tracking of Red Kites (*Milvus milvus*) reveals fledgling number is negatively correlated with home range size. *Journal of Ornithology*, 156 [4], pp. 963–975. DOI: 10.1007/s10336-015-1230-5.
- Pistorius, PA. ; Hindell, MA. ; Tremblay, Y. ; Rishworth, GM.** (2015). Weathering a Dynamic Seascape. *PloS one*, 10 [11], pp. e0142623. DOI: 10.1371/journal.pone.0142623.
- Powell, RA** (2000). Animal Home Ranges and Territories and Home Range Estimators, pp. 65–110. In: Research Techniques in Animal Ecology. Boitani, L; Fuller, TK. Columbia University Press. New York.
- Powell, RA. & Mitchell, MS.** (2012). What is a home range? *Journal of Mammalogy*, 93 [4], pp. 948–958. DOI: 10.1644/11-MAMM-S-177.1.
- R Core Team (2017). R. R Foundation for Statistical Computing, Vienna, Austria.
- Ratcliffe, N. ; Takahashi, A. ; O'Sullivan, C. ; Adlard, S. ; Trathan, PN. ; Harris, MP. ; Wanless, S.** (2013). The roles of sex, mass and individual specialisation in partitioning foraging-depth niches of a pursuit-diving predator. *PloS one*, 8 [10], pp. e79107. DOI: 10.1371/journal.pone.0079107.
- Rivrud, IM. ; Loe, LE. ; Mysterud, A.** (2010). How does local weather predict red deer home range size at different temporal scales? *The Journal of animal ecology*, 79 [6], pp. 1280–1295. DOI: 10.1111/j.1365-2656.2010.01731.x.
- Rosenberg, DK. ; Swindle, KA. ; Anthony, RG.** (2003). Influence of prey abundance on northern spotted owl reproductive success in western Oregon. *Canadian Journal of Zoology*, 81 [10], pp. 1715–1725. DOI: 10.1139/z03-167.

- Säid, S. ; Gaillard, JM. ; Widmer, O. ; Débias, F. ; Bourgoïn, G. ; Delorme, D. ; Roux, C.** (2009). What shapes intra-specific variation in home range size? *Oikos*, 118 [9], pp. 1299–1306. DOI: 10.1111/j.1600-0706.2009.17346.x.
- Santangeli, A. ; Hakkarainen, H. ; Laaksonen, T. ; Korpimäki, E.** (2012). Home range size is determined by habitat composition but feeding rate by food availability in male Tengmalm's owls. *Animal Behaviour*, 83 [4], pp. 1115–1123. DOI: 10.1016/j.anbehav.2012.02.002.
- Schifferli, L. ; Gruebler, MU. ; Meijer, HAJ. ; Visser, GH. ; Naef-Daenzer, B. ; Reynolds, J.** (2014). Barn Swallow *Hirundo rustica* parents work harder when foraging conditions are good. *IBIS*, 156 [4], pp. 777–787. DOI: 10.1111/ibi.12186.
- Sergio, F.** (2003). From individual behaviour to population pattern. *Animal Behaviour*, 66 [6], pp. 1109–1117. DOI: 10.1006/anbe.2003.2303.
- Sieder, S** (04/2018). Fast food, slow birds – a trade-off between foraging and nest attendance modulates parental mobbing in a long-lived raptor, Wien.
- Staggenborg, J. ; Schaefer, HM. ; Stange, C. ; Naef-Daenzer, B. ; Gruebler, MU. ; Sanchez-Zapata, JA.** (2017). Time and travelling costs during chick-rearing in relation to habitat quality in Little Owls *Athene noctua*. *IBIS*, 159 [3], pp. 519–531. DOI: 10.1111/ibi.12465.
- Strong, AM. & Sherry, TW.** (2000). Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. *The Journal of animal ecology*, 69 [5], pp. 883–895. DOI: 10.1046/j.1365-2656.2000.00447.x.
- Sunde, P. ; Thorup, K. ; Jacobsen, LB. ; Rahbek, C.** (2014). Weather conditions drive dynamic habitat selection in a generalist predator. *PloS one*, 9 [2], pp. e88221. DOI: 10.1371/journal.pone.0088221.
- Swiss Ornithological Institute** (2017). Mechanisms of population dynamics in Red Kites. <http://www.vogelwarte.ch/en/projects/ecological-research/mechanisms-of-population-dynamics-in-red-kites>. 17.03.2018.
- Wasmund, N** (2013). Der Rotmilan (*Milvus milvus*) im Unteren Eichsfeld. Brutbestand, Nahrungsökologie und Gefährdungsursachen., Göttingen.
- Weimerskirch, H. ; Le Corre, M. ; Ropert-Coudert, Y. ; Kato, A. ; Marsac, F.** (2006). Sex-specific foraging behaviour in a seabird with reversed sexual dimorphism. *Oecologia*, 146 [4], pp. 681–691. DOI: 10.1007/s00442-005-0226-x.
- Zabel, CJ. ; McKelvey, K. ; Ward, JP.** (1995). Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (*Strix occidentalis caurina*). *Canadian Journal of Zoology* [73], pp. 433–439.

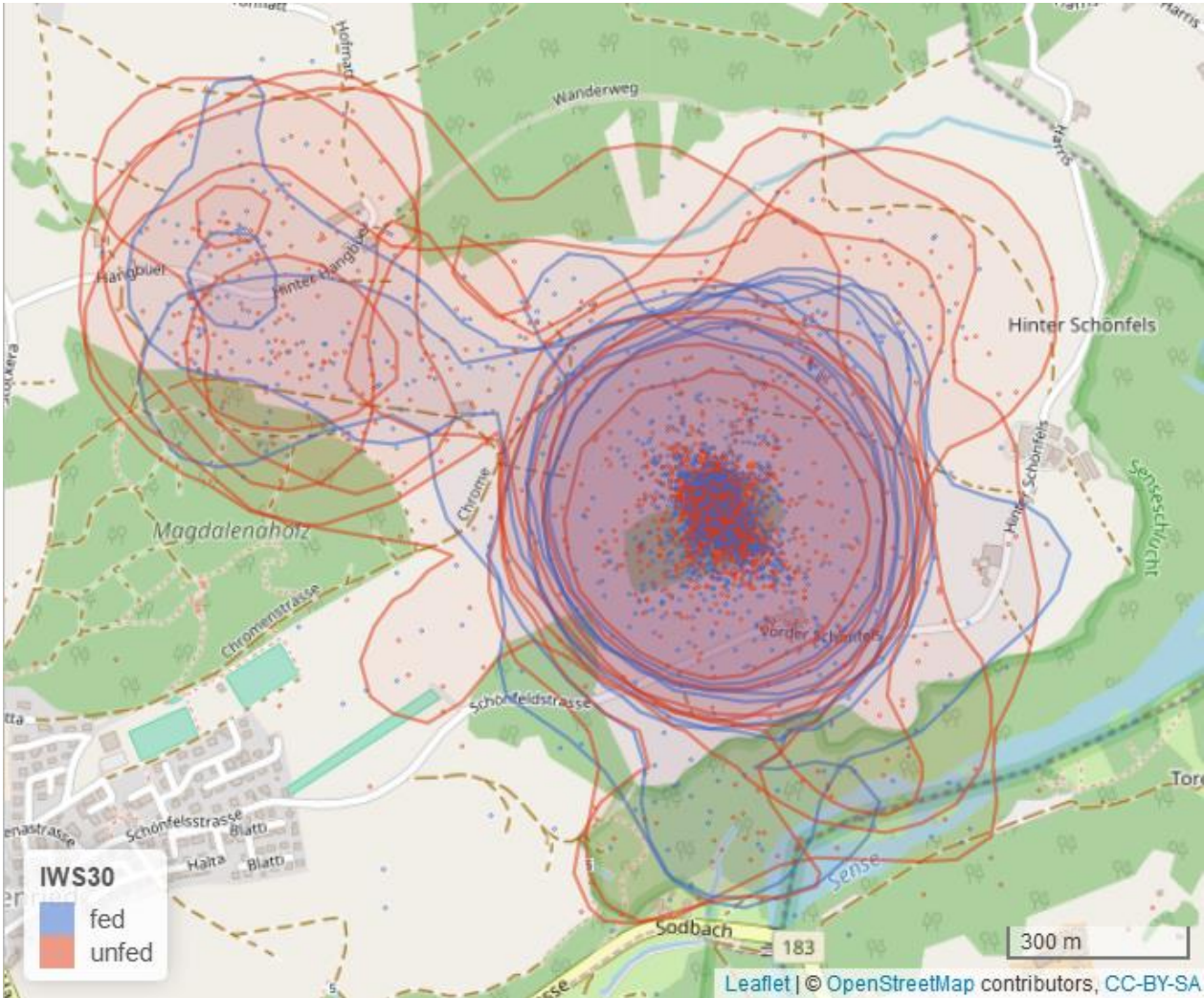
8. Appendices

Appendix 1: Overview table of each bird per nesting period given the year, sex, nest, feeding days (feeding), number of home ranges (Nbr. hr), mean daily home range size ($\bar{\varnothing}$ hr in km²) with standard deviation (sd), full breeding attempt kernel home range size (hr season in km²) and full breeding attempt minimum convex polygon (MCP in km²) with amount of GPS fixes they were calculated from (GPS fixes).

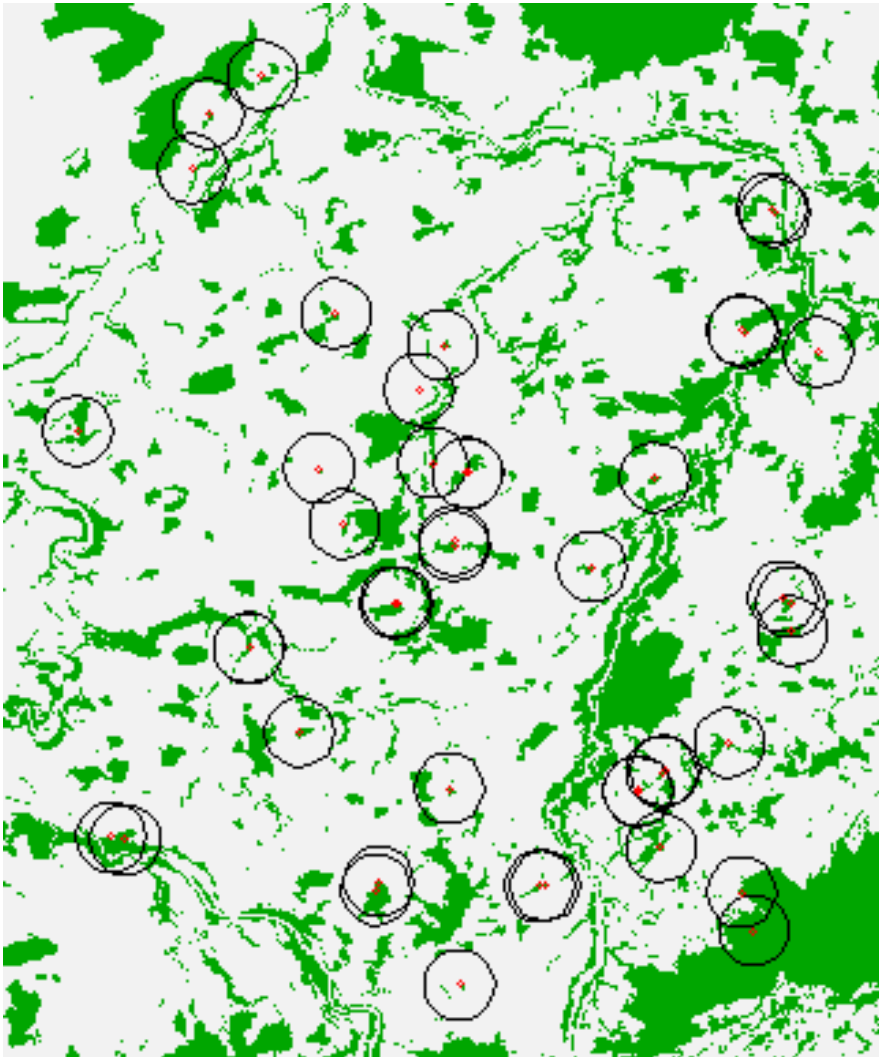
ID	year	sex	nest	feeding	Nbr. hr	$\bar{\varnothing}$ hr	sd	hr season	MCP	GPS_fixes
IWS10	2016	f	20	5	11	1.273	0.622	2.0988	2.4334	5773
IWS24	2016	f	36	14	23	0.678	0.243	0.756	1.0875	11570
IWS24	2017	f	38	19	37	0.946	0.842	1.1736	2.628	18488
IWS30	2017	f	31	7	14	0.593	0.319	0.7056	0.8587	7147
RKA07	2017	f	19	15	32	0.926	0.532	1.4724	2.1554	13860
SIU16	2016	f	37	1	4	1.358	0.859	1.926	2.0348	2454
SIU23	2017	f	21	23	41	0.512	0.193	0.6264	0.6873	19541
SIU24	2016	f	12	7	19	0.659	0.251	0.8604	1.0335	8662
SIU27	2017	f	7	17	33	0.683	0.402	0.9576	2.5408	15638
SIU28	2016	f	16	2	5	0.785	0.136	0.8568	0.9773	2270
SWU01	2017	f	25	23	44	0.576	0.492	0.7092	0.6192	20446
IWS04	2016	m	20	12	25	1.606	0.509	2.2752	2.6342	11908
IWS05	2017	m	25	2	5	2.597	0.853	3.384	8.0598	2577
MLR15	2017	m	38	19	38	3.288	2.875	7.4808	6.4312	18548
MLR15	2016	m	36	24	42	2.633	1.113	3.7944	12.9496	20271
REK08	2017	m	17	3	6	1.607	0.594	1.9836	3.2929	2326
REK22	2017	m	19	14	29	2.606	0.685	3.3732	5.3428	13017
SIU14	2017	m	26	29	57	2.875	1.924	9.9216	19.3149	27388
IWS25	2016	f	11	0	8	1.245	0.383	1.4796	3.2642	3650
REK05	2017	f	44	0	31	0.399	0.162	0.4824	0.4893	14621
REK20	2017	f	18	0	12	1.202	0.641	3.6072	26.7156	6295
REK23	2017	f	1	0	12	1.577	0.533	2.2356	3.4223	5216
REK25	2017	f	28	0	11	2.995	1.419	6.0156	18.4809	4919
RKA05	2017	f	32	0	1	0.641	NA	0.576	0.4083	937
RKA14	2017	f	8	0	8	0.438	0.198	0.45	0.3184	4834
RKI17	2017	f	10	0	10	1.331	0.836	1.7496	3.1447	4555
SIU03	2016	f	9	0	21	1.292	0.622	1.8324	2.346	9054
SIU07	2016	f	41	0	9	0.589	0.303	0.6624	0.9434	4240
SIU07	2017	f	40	0	14	0.317	0.082	0.2952	0.0979	6012
SIU16	2017	f	39	0	22	1.016	0.534	1.3284	0.3896	10956
SIU18	2016	f	23	0	10	1.913	1.853	2.1312	10.6932	6313

SIU23	2016	f	22	0	26	0.661	0.159	0.792	1.2482	12433
SIU27	2016	f	6	0	15	1.284	0.356	1.5156	2.4508	7014
SIU28	2017	f	15	0	2	0.227	0	0.4572	0.3766	2329
SIU29	2016	f	14	0	5	0.9	0.485	1.2672	1.2802	3387
SIU29	2017	f	13	0	19	0.463	0.201	0.5364	0.4745	8830
SWU01	2016	f	24	0	10	1.23	0.496	1.6992	1.0491	4823
IWS03	2016	m	43	0	8	6.959	4.915	20.2104	57.5095	3951
IWS03	2017	m	42	0	32	4.84	3.198	13.8276	20.1766	15752
IWS05	2016	m	24	0	10	2.349	0.905	3.2184	3.2349	4871
IWS14	2016	m	41	0	9	2.504	0.642	3.2364	3.6124	4437
IWS14	2017	m	40	0	25	1.895	0.501	2.2104	2.7042	12298
IWS28	2016	m	33	0	12	1.538	0.515	2.1096	3.2788	5495
IWS28	2017	m	34	0	26	1.204	0.6	1.2888	1.1785	12500
REK17	2017	m	5	0	14	3.755	1	5.5512	12.5816	6469
RKA12	2017	m	45	0	15	1.552	0.276	1.7496	1.7376	7342
RKA15	2017	m	4	0	1	3.65	NA	3.6468	3.5995	324
RKA18	2017	m	44	0	4	1.502	0.138	1.6848	1.9831	1708
SIU06	2016	m	29	0	32	0.715	0.519	0.7128	1.5055	15281
SIU06	2017	m	30	0	21	0.656	0.253	0.756	0.5225	10273
SIU14	2016	m	27	0	19	3.17	2.664	8.1936	19.3149	9038
WIK07	2016	m	2	0	15	2.516	1.824	4.248	6.4233	6972
WIK07	2017	m	3	0	5	2.682	0.964	3.9168	5.8487	2433

Appendix 2: Daily home ranges of bird IWS30 in 2017 on fed (blue line) and unfed days (red line) visualized in © OpenStreetMap via leafletR (Graul 2016).



Appendix 3: Forest raster layer (25 x 25 m) with nest locations (red dots) and buffer circle (black circles).



Appendix 4: Effect plot of temperature (°C) on daily home range size (km²). Intercept at 1.55 km² and slope 0.0038.

