# Sex-specific foraging niches and habitat selection in an

## asynchronously breeding bird, the European hoopoe

Upupa epops

**Master thesis** 

Faculty of Science, University of Bern

Handed in by:

Roman H. Bühler

2016

Supervisors:

Dr. Alain Jacot

Prof. Dr. Raphaël Arlettaz

#### Sex-specific foraging niches and habitat selection in an asynchronously breeding bird, the

European hoopoe Upupa epops

Roman H. Bühler<sup>1</sup>, Raphaël Arlettaz<sup>1,2</sup>, Alain Jacot<sup>1,2</sup>

<sup>1</sup> Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland

<sup>2</sup> Swiss Ornithological Institute, Field Station Valais, 1950 Sion, Switzerland

#### Abstract

In order to reduce interspecific exploitative competition and to partition ecological space, species differ in their patterns of resource use, notably in their habitat and trophic niche: they often show variation in dietary composition, obtained from different foraging habitats. Even within species, sexspecific divergence in resource exploitation patterns has been observed, often associated with sexual dimorphism. Using GPS technology and video surveys, we investigated sexual differentiation in patterns of habitat selection and prey exploitation in the hoopoe, a non-passerine bird with slight sexual dimorphism. Male and female hoopoes differed in their patterns of habitat selection in intensively managed fruit tree cultures, most likely as a consequence of different prey preferences. While females delivered smaller prey items to chicks, in particular various types of larvae, males provisioned above all molecrickets of large size. In the farmland matrix, females tend to avoid pear plantations as well as a high amount of litter in the middle row between the fruit trees; they further showed a preference for cultures harboring a high diversity and abundance of invertebrates, probably because this increases foraging opportunities. Males mainly visited fruit tree plantations exhibiting a high amount of bare ground underneath the trees, which has been shown to enhance molecricket accessibility; they also showed preference for cultures with higher insect richness than average. Males furthermore foraged further away from the nest than females. This difference in foraging distance is likely in response to male's preference for molecrickets that occur in clustered local hotspots. We hypothesize that the asynchronous hatching of hoopoes leads to a need to provision prey of different size with respect to nestling age, which may result in niche segregation between the two genders. As this need for different types of prey is restricted to a certain brood stage, the observed niche separation could be only temporary.

#### Keywords

European hoopoe, *Upupa epops*, sex-specific, forging niche, dimorphism, habitat selection, interspecific competition

#### Introduction

Direct benefits accrued through food are fundamental components determining individual reproductive success and lifetime fitness (Gasparini *et al.* 2006; Class & Moore 2013). Important aspects of food resource use range from prey abundance, prey type to prey availability, where selection is expected to minimize interspecific exploitative competition in space and time (Ricklefs & Miller 1999). In several cases not only species will differ in resource exploitation, but selection will additionally promote foraging niche separation between sexes within one species (Le V. dit Durell, Goss-Custard & Caldow 1993; Radford & Du Plessis 2003; Stenberg & Hogstad 2004; Temeles, Miller & Rifkin 2010).

Such sex-specific differences in patterns of habitat selection and prey exploitation might have evolved indirectly as a consequence of evolutionary adaptations acting on a different trait. Sexual selection for large litter size and thus large females can lead to intersexual dietary divergence as has been demonstrated in several snake species (Houston & Shine 1993) and spiders (Pekár, Martišová & Bilde 2011). In contrast, sexual selection can also lead to larger males via male-male competition or female mate choice and its concomitant effects on dietary specialisation in relation to gender (e.g. anoles lizard: Perry (1996); grey seal: Beck, Iverson & Bowden (2005)). In birds, this topic has first been addressed by Selander (1966) followed by studies in new world blackbirds (Webster 1997), black-tailed godwits (Catry *et al.* 2012) and the great bustard (Bravo *et al.* 2016). In all those species showing a high sexual

dimorphism, it has convincingly been demonstrated that the sexes differ in foraging behaviour, which seems to be induced by sexual selection processes. However, intersexual dietary specialization, i.e. an adaptive divergence of foraging niches between the sexes can also arise under other specific ecological contexts.

In cooperative breeders individuals forage in close-knit groups resulting in high competition for food between individuals. Avoiding such competition may result in partitioning of ecological space between sexes, which then translates into differences in bill morphology, as has been suggested in green woodhopooes, *Phoeniculus purpureus* (Radford & Du Plessis 2003). Alternatively, competition for scarce and patchy food resources may exert distinct selective forces on the two sexes and lead to a segregation of foraging niches. In nectar feeding hummingbirds, there are multiple examples where males and females show strong differences in bill morphology which leads to an ecological separation, i.e. a specialization on different flower types (Temeles, Miller & Rifkin 2010). Interestingly such consistent differences in foraging ecology between the sexes often go hand in hand with high dimorphism, especially in trophic morphological structures such as the bill (Selander 1966; Shine 1989).

Hatching asynchrony, a breeding system leading to a size hierarchy among the nestlings (Stenning 1996), could be another ecological context that promotes sex-specific foraging preferences. In highly asynchronous broods, parental birds have to allocate prey towards nestlings which differ in size, age, hunger state and competitive ability, and a specialization of sex-specific feeding patterns has been indicated in the European hoopoe (Guillod, Arlettaz & Jacot 2016a; Ryser *et al.* 2016). Previous studies have showed that hoopoe male and female parents feed their hatchlings differentially: While males seem to preferentially feed the older nestlings with large prey items (mainly molecrickets, *Gryllotalpa gryllotalpa*), females often enter the nest box and feed all nestlings with smaller and more diverse prey items (Guillod, Arlettaz & Jacot 2016a; Ryser *et al.* 2016). As younger and smaller nestlings are not able to swallow big prey (Wiebe & Slagsvold 2009), the behaviour of females to specialize on smaller prey could reflect an adaptive, compensatory feeding behaviour that maximises reproductive success. While

unknown how this divergence translates into differences in foraging behaviour and habitat preferences. A recent study indeed indicates a selection of certain habitat characteristics, such as the amount of bare ground, but the study was based on males only (Tagmann-Ioset *et al.* 2012).

In this study we investigate the behaviour and habitat preferences during foraging of male and female hoopoes when size differences among the chicks are highest. In line with previous findings (Tschumi, Schaub & Arlettaz 2014; Guillod, Arlettaz & Jacot 2016), we predict that males, which specialize on molecrickets, exploit foraging grounds further away from nest than females because molecricket occurrence is patchy in space. In contrast, females, which bring various smaller prey (Guillod, Arlettaz & Jacot 2016a; Ryser *et al.* 2016), are expected to occur more randomly in space and should therefore be found closer to the nest box. These data should highlight how sex-specific foraging niches can translate into variation in foraging behaviour or habitat preferences and the findings could ultimately be used for improving habitat management for species conservation.

#### **Material and Methods**

#### Study area

The study took place in the upper Rhône valley in Valais (South-western Swiss Alps, WGS 84: 46.18107, 7.21784) from April to July 2015. The study area (~70 km<sup>2</sup>) is dominated by industrial farming, mainly fruit tree plantations interspersed by very few vineyards, crop plantations and greenhouses. Pear, apple, apricot, plum and cherry fruit trees are the most common type of culture, where trees are aligned in parallel rows. The habitat on the ground level mainly consists of lines of bare ground under the trees, often treated with herbicides, and more or less vegetated lines between the tree rows. These vegetated middle rows are mown regularly, specifically before pesticide treatments in order to avoid negative collateral effects on pollinating species.

#### Study species

Hoopoes *Upupa epops* are non-passerine, secondary cavity breeding migratory birds, which inhabit semi-open, dry and sunny habitats (Cramp 1985) as provided in the Rhone valley in Valais. Hoopoe females start incubating from the first, second or even third egg, which results in asynchronous hatching and size differences of the offspring (Martín-Vivaldi *et al.* 1999). In the first week after the first chick has hatched, only the male provisions food to the nestlings and to the brooding female (Martín-Vivaldi *et al.* 1999). After that, also the female starts to forage and to feed the chicks (Martín-Vivaldi *et al.* 1999). Overall, molecrickets are the dominant prey item (Fournier & Arlettaz 2001; Barbaro *et al.* 2008; Schaub *et al.* 2010; Tagmann-loset *et al.* 2012) but specifically females also feed diverse insect larvae, spiders and other small prey items to the chicks (Glutz von Blotzheim & Bauer 1980). In a previous study we have shown that males mainly feed large molecrickets to older and larger chicks, while females have a more even feeding pattern and are more likely to feed small hungry chicks, usually with smaller prey items (Ryser *et al.* 2016). The present study focuses on this time window (age of oldest chick: 10-12 days) when the sizes between nestlings differ strongly and food demand of the chicks is highest (Arlettaz *et al.* 2010a).

The hoopoe population in Switzerland suffered from a strong decline until 1990 where the installation of 700 nest-boxes at about 370 locations in the Rhône plain led to a remarkable, 6-fold increase of the local hoopoe population (Arlettaz *et al.* 2010b). To determine if occupied, all nest-boxes were inspected every other week throughout the breeding season (march – august). Once a nest-box was found occupied it was checked every 3 days to collect data about clutch size, hatching date and number of fledglings. To avoid excessive disturbance, the controls were realised by entering a small mirror trough the entrance hole. For each brood that was used in the current study we installed dummy equipment at least one week before catching (inside video camera, outside photo camera and spring trap) in order to habituate the birds towards the new equipment. The catching of the adults started when the oldest nestling was around 12 days old. We aimed at catching both adults the same day using several techniques (mist net, spring trap and taken directly from nest)

since we wanted to record habitat use of both parents at the same day. Females were marked by coloring part of the head feathers, this to facilitate the later identification of the sexes when analyzing the photo and video footage (Ryser *et al.* 2016).

#### Sex-specific habitat use

In order to analyse sex-specific habitat use of hoopoes, we aimed at recording both adult birds within a pair at the same day (pairs caught same day: 9, different days: 1, single birds: 2). Each adult bird was equipped with a logger (Robin mobile unit 4, Cell Guide, Israel; 3.7g) set to start recording datapoints (1 fix/90 s.) on the next day from 5AM to 22PM. Only adult birds heavier than 60 g were chosen to be equipped. Each logger was mounted with an elastic leg-loop harness, which was individually adaptable to the birds' size. Each bird was recaptured two days after catching, when the recording period was over, either again on the nest, using mist nets or with spring traps and the logger including the leg-loops were removed.

Data of the logger were extracted the same day and visualized on GIS software QGIS (QGIS Development Team 2015). To avoid analysing inaccurate locations we only included data points that had a signal to noise ratio (SNR) higher than 38 (Ryan *et al.* 2004). In a next step we selected, based on data points, the four most visited parcels, later called "presence parcels". The number of locations of these presence parcels ranged from 5 to 100 data points. In order to analyze habitat preferences we had to compare selected (used) versus non-selected (available but unused) parcels. These non-selected parcels are also called pseudo-absence parcels, since they were not visited during the study but we cannot guarantee that they were not visited during another timespan. The corresponding pseudo-absence parcels had to be adjacent to the presence parcel and had to show no or few (<5) GPS-points on it. Both, presence and pseudo-absence parcels were mapped as soon as possible, between 1 to 4 days after the birds had been equipped with a logger. For each parcel we measured invertebrate abundance and diversity and the structure of the vegetation. To assess invertebrate abundance and diversity we randomly placed 2 pitfall traps per parcel active for 7 days each (92.5 mm diameter; 1:3 water and propyleneglycol (1,2 propandiol) adding natriumdodecylsulfat to further

reduce surface tension). Pitfall traps were placed at the interface between the herbicide treated line underneath the trees and the vegetated middle row. The arthropod samples were identified to the following levels: coleoptera, opiliones, other arachnida, hymenoptera, saltatoria, cicadina, heteroptera, diptera, dermaptera, mollusca, lepidoptera, larvae, others. The animals were identified with help of magnification glasses or stereomicroscope if needed, and afterwards stored in 70% ethanol. We merged the data from the two traps and calculated overall abundance and group diversity, as well as the Shannon diversity index for every parcel. The Shannon diversity index was calculated additional to the group diversity, because it combines two separate aspects of diversity in one factor: richness and evenness (Nagendra 2002). We choose the Shannon index mainly because this index is equally sensitive to rare and common species (Morris *et al.* 2014). Two traps with a dead mouse were excluded from further analysis.

Vegetation structure was quantified on four 1m<sup>2</sup> squares per parcel. We always quantified the vegetation structure next to the pitfall traps, one plot in the vegetated middle row and one trap in the mostly bare row underneath the trees. The following variables were quantified: cover of vegetation, bare ground, litter and stone (sums up to 100%) and mean vegetation height. For data analysis the two measurements underneath the trees and the two in the middle row were merged by taking the mean (for values see Table 1). Additionally we recorded the following variables at the parcel scale: plantation type (apple, pear, apricot, others) and the mean height of the trees.

#### Sex-specific feeding patterns

Once the birds were equipped with the GPS logger we exchanged the dummy equipment with the real equipment. The video system inside the nest box consisted of one black/white infrared camera (Conrad, CMOS B/W camera with IR light; lens: 3.6mm), which was installed in the nest box lid and connected to a solid-state recorder (Lupus, Aeon MDVR). Both were powered via a multi plug (MW, Multiplier) and voltage transformers (Voltcraft, SMP20A) by a 12V battery (Conrad Energy, 10 Ah, CP12120). While the inside camera recorded all feeding events inside the box, parents sometimes also feed from the nest entrance, i.e. they do not enter the box. To record as much feeding events as

possible, we additionally installed a trail camera (Reconyx type PC900) outside of the nest box next to the entrance hole. For each feeding event we recorded the sex of the feeding parent, the prey brought by the bird and time of arrival and departure.

#### Statistical analysis:

All analysis were performed in R under version 3.3.1 (R Development Core Team 2016) and raw outputs are presented in the results section.

To analyse the GPS data, we first calculated the distance from the nest-box to the points recorded for every individual by using the function *pointDistance* from the package *raster* (Hijmans *et al.* 2015). In a second step we analysed feeding bouts for every individual: With the help of the photo and video data we were able to analyse at which time the birds return to the nest and what sort of prey they brought. We then assigned all the points between two feeding events to one feeding bout. All feeding bouts were then visualized and obvious outlier points, such as single points with low SNR and appear at high distance to following/previous points, within the bouts were removed. We additionally removed all first loops from the analysis, as we couldn't be sure at which time the bird started to forage in the morning, as well as bouts only incorporating one point. Because feeding activity differs all along the day (Guillod, Arlettaz & Jacot 2016a), we always made sure to incorporate the same time window for both sexes within a pair in our analysis. For every bout the maximal, mean and median bout distance to the nest was calculated by using the package plyr (Wickham 2011). To analyse we used linear mixed effect models, fitted with the function Ime from the R-package nlme (Pinheiro et al. 2012): maximal, mean or median distance served as response variable, sex as explanatory variable and territory as well as bird identity were incorporated as random effects. Adding these random effects helps to avoid potential pseudo-replication effects caused by non-independent data and allows analysing all individuals simultaneously (Gillies et al. 2006). To improve model fit the response variables were log transformed, as they were left skewed initially. We used a kernel density estimator to calculate home range area from all data points for every bird by using the function kernel.area from the R package adehabitatHR (Calenge 2006;

Calenge 2007). We calculated kernel densities encompassing 95% as well as 50% of the maximum density as we were interested in the size of the overall area used (95%) as well as in the size of the area with increased density of points (50%). To test whether area differs between the sexes we again used linear mixed effect models with area as response variable, sex as explanatory variable and territory as random effect by using the function *lme* (Pinheiro *et al.* 2012). Number of provisioned molecrickets and number of larvae were analysed by running hierarchical logistic regression models (GLMM) with binomial error distribution and a logit link function. Prey type frequency was incorporated into the model using the function *cbind* (number of certain prey item/ total number of items) and served as response variable, while sex was the explanatory variable and pair was incorporated as random factor. For this part of the analysis we used the function *glmer* of the R-package *lme4* (Bates *et al.* 2015). We also tested the number of total feeding events depending on sex, by fitting a linear mixed effect model with the function *lme* (Pinheiro et al. 2012) including territory as random effect.

To evaluate the habitat selection we compared the ground cover, vegetation and invertebrate variables (see Table 1) between presence and pseudo-absence parcels. To do so, we used hierarchical logistic regression models (GLMM) with binomial error distribution and a logit link function where we included bird identity and parcel identity as random effects. Habitat and invertebrate data were incorporated as fixed effects (for factors see Table 1) and the models were fitted using *glmer* function of the R-package *lme4* (Bates *et al.* 2015). The variable "stones" was excluded from the analysis as it contained >90% of zero values. Right skewed variables were log transformed and to facilitate the later interpretation of the model coefficients of all variables were standardized, meaning that the mean was subtracted from every value and the value then divided by the standard deviation. For ground cover variables we also included the quadratic term as we expected possible curvilinear relationship to occurrence probability (Schaub *et al.* 2010; Tagmann-loset *et al.* 2012). To avoid collinearity we checked all continuous variables by calculating their Spearman correlation coefficient |r|. Based on univariate models we dropped the least significant

variables if their correlation coefficient was >0.7 (Hosmer & Lemeshow 1989). To test which variables might play a role in our final model, we fitted a univariate model of every variable predicting occurrence probability. If the p-value was <0.2 in the univariate model we kept the variable for further modelling. Out of the variables left we generated a list of candidate models, by using the function *dredge* from the package *MuMIn* (Bartoń 2016). The dredge function allows testing every possible combination and thus to detect the most supported models by ranking them by AICc (Akaike Information Criterion with correction for small samples). Our set of competitive models was chosen according to the  $\Delta$ AICc which had to be <2 from the first ranked. Corresponding AICc weights were calculated which show the probability of the models to be the best one among the set of competitive models (Burnham & Anderson 2002). Occurrence probability was plotted against one of the variables, while setting the other variables of the model to the mean. The 95% credible interval of the regression line was obtained by 10 000 times simulating the posterior distribution and its 2.5% and 97.5% quantiles with package *arm* (Gelman *et al.* 2015).

Further we fitted linear models (Im) to test if arthropod abundance, arthropod richness, Shannon index and insect richness differs significantly between the plantation types (apple, apricot, pear, others).

#### Results

#### Sex-specific foraging niche

In total we recorded 649 feeding bouts (females: 301, males: 348) and 710 food deliveries from which we were able to identify the prey type in 570 cases. For the 12 territories we had on average 54±35 feeding bouts per territory and a mean of 25±19 bouts for every of the 22 birds. Overall, prey items consisted of 55% molecrickets (N=313), 44% of insect larvae (N=252) and 1% of other prey items (3 spiders, 1 field cricket *Gryllus campestris*, 1 snail). In proportion to delivered prey items, males brought significantly more molecrickets compared to females (1.19±0.31, z=3.89, p=<0.001)

whereas females allocated more larvae to their chicks compared to males (0.99±0.3, z=3.32, p=<0.001). Feeding rates did not differ between the sexes (4.15±5.77,  $t_{21}=0.719$ , p=0.5).

When foraging, males traveled significantly further away from the nest box than females ( $0.39\pm0.13$ ,  $t_9=3.06$ , p=0.014, Fig. 4): regarding predicted mean bout distance females travel 107m (95 CI: 69-165m) and males 159m (95% CI: 103-244m), which is around 67% further. This pattern is also shown taking median distance ( $0.47\pm0.13$ ,  $t_9=3.17$ , p=0.011), however not reflected by maximal distance within a foraging bout ( $0.3\pm0.14$ ,  $t_9=2.17$ , p=0.06).

#### Sex-specific habitat use

In total, we obtained 14032 locations, i.e. on average  $561\pm172$  locations per bird (range: 52-703), from which 9703 or 69% were of good quality (SNR higher than 38). For every of the 22 birds 4 presence and 4 pseudo-absence parcels were chosen, except for one female were we could identify 3 presence parcels only, resulting in 191 selected parcels (presence: 95, pseudo-absence: 96). These parcels consisted to 62% of apple plantations (N=118), 19% were pear plantations (N=37), 17% apricot plantations (N=33) and 2% of other type (N=3). While arthropod richness (0.46±0.2,  $t_{176}$ =2.3, p=0.02) and abundance (0.42±0.2,  $t_{176}$ =2.1, p=0.04) were significantly higher in apricot parcels compared to apple, it did not differ between the other plantations (all p>0.05, for values see Table 4). Further there was no difference between the plantation types concerning Shannon index (all p>0.05, for values see Table 4) and insect richness (all p>0.05, for values see Table 4). Parcels showed in mean 35% bare ground, 45% of vegetated area and 20% were covered by litter.

Home ranges were, on average  $0.52\pm0.83$  km2 (range: 0.02-3.27 km2) with 95% density estimation and  $0.1\pm0.18$  km2 (range: 0.002-0.788 km2) with 50% density estimation and did not differ among the sexes (95%:  $0.21\pm0.33$ ,  $t_{22}=0.64$ , p=0.53; 50%:  $0.14\pm0.36$ ,  $t_{22}=0.4$ , p=0.69). For graphical representation of the home ranges with 95% density estimation see Appendix Figure 1.

Females preferred parcels with a high arthropod diversity (Shannon diversity index,  $3.77\pm1.3$ , z=2.92, p=0.003, Fig. 1), a reduced amount of litter in the middle row (-1.59±0.95, z=-1.68, p=0.093) and

avoided pear plantations (-1.38 $\pm$ 2.47, z=-2.05, p=0.04, reference=apple). Competitive models ( $\Delta$ AICc<2) also included a positive effect of a higher amount of vegetation in the middle row, see table 3 for a list of the candidate models.

Male hoopoes showed a preference for parcels with a high insect richness ( $0.43\pm0.22$ , z=1.95, p=0.05, Fig. 2) and high amounts of bare ground underneath the trees ( $0.37\pm0.22$ , z=1.64, p=0.10, Fig. 3). Other candidate models also included amount of litter under the trees, as well as its quadratic term (see table 3 for a list of the candidate models).

#### Discussion

This study highlights that males and females differ in their foraging strategy when their chicks show a high degree of size differences. Males travel further and bring large molecrickets, while females forage closer to the nest cavity and bring smaller prey items, mainly larvae. These differences may partly explain the observed variation in habitat preference. Within their range, males selected parcels with a combination of elevated amounts of bare ground underneath the tree and high insect richness, whereas female occurrence is best explained by parcels having a diverse arthropod fauna, the type of plantation and low amounts of litter in the middle row.

These patterns all suggest that males and females differ in resource exploitation during this nestling period. The adaptive explanation of these sex-specific foraging niches can best be understood by the hoopoes breeding behavior. As has been demonstrated by Ryser et al. (2016), males mainly feed large molecrickets from outside the nest box and the food is allocated to the most dominant chicks that can monopolize the nest entrance. As has been shown, molecrickets are the most profitable prey species locally (Fournier & Arlettaz 2001; Guillod, Arlettaz & Jacot 2016b) and from an optimal foraging's perspective it may pay to fly longer distances even if molecrickets occur patchily in space (Stephens & Krebs 1986). In contrast, females show a much more even food distribution and allocate smaller prey to the neediest chicks, which are very often the smallest subdominant individuals (Ryser

*et al.* 2016). The fact that large prey cannot be swallowed by the youngest chicks (Wiebe & Slagsvold 2009; own observations) is resulting in a need of smaller prey provided by the female bird (Slagsvold & Sonerud 2007). Such smaller prey items, in our study mainly insect larvae, may occur more random in space, which may explain the shorter forging distances of females. Home ranges, including all data points within the recorded time period, did not differ between the sexes. While there was a tendency that males showed slightly bigger home range, the time span of one day might be too short to capture the whole extent of sex-specific differences in spatial habitat use. Those findings of sex-specific foraging behavior are partly mirrored by differences in habitat preferences of the two sexes.

Both, males and females showed a preference for certain parcel characteristics i.e. visited parcels differed from adjacent non-visited parcels. For female birds, the model best predicting its occurrence on a parcel included the Shannon index of invertebrates (Figure 1), plantation type and the amount of litter in the middle row. While the invertebrates caught in the pitfall traps may only vaguely reflect the hoopoes' prey composition, we assume that the Shannon index is a good proxy for the general invertebrate biodiversity of a parcel. The higher the index, the more diverse and abundant the invertebrate community and the more likely it is for female birds to find suitable food items, such as caterpillar and coleopteran larvae. Considering plantation type, females showed a significant avoidance of parcels planted with pear trees. Given the non-significant difference in abundance and diversity of arthropods between pear and other plantations, it is more likely that other plantation characteristics such as specific management practices may affect female occurrence. The negative impact of the amount of litter in the middle row could be explained by the lower accessibility of the prey. Additional structures in the middle row may represent an obstacle for hoopoes foraging tactic when probing the upper strata of the soil for prey with their bill. Future studies investigating the effect of management practices in fruit tree plantations on the diversity and abundance of invertebrates merit more attention and could help improving suitable habitats for insectivorous ground-foraging bird species (Schaub et al. 2010).

Our result that bare ground plays an important role in male parcel selection is in line with the findings of Tagmann-loset et al. (2012), which showed the importance of bare ground at the foraging scale. An elevated amount of bare ground is important for the accessibility of prey items, especially ground dwelling arthropods such as molecrickets (Tagmann-loset et al. 2012). In our study, bare ground especially under the trees seem to play an important role, which could be explained by the higher density of tree roots, one of the main food sources of molecrickets (Baur et al. 2006). The finding that bare ground increases food detectability and thereby its accessibility should not be restricted to hoopoes but has repeatedly been shown in insectivorous birds in a variety of agricultural habitats (Schaub et al. 2010). Insect richness, another factor in our best model, indicates parcels with higher abundance of arthropod prey and might be directly correlated with the main prey the molecricket. Because molecricket abundance is very difficult to directly assess at parcel scale, we were not able to account for this factor in our study. This is unfortunate, since a recent study was able to show the importance of molecricket abundance on territory occupancy and reproductive success (Guillod, Arlettaz & Jacot 2016a). Molecricket abundance being such an important driver of hoopoe reproductive success, we are confident that adding a direct measure of molecricket abundance would significantly improve our models of male occurrence. Even adding indirect parameters explaining molecricket occurrence such as soil type, soil density and depth of groundwater table could help explaining better a males habit selection (Tschumi, Schaub & Arlettaz 2014). This would additionally allow delineating and conserving such molecricket rich areas, which could be crucial for the long-term persistence of the hoopoe population.

Our study highlights the importance of focusing on both sexes in habitat selection studies, especially in regard to conservation related issues. Often, habitat selection studies are based on one sex only (Menz, Mosimann-Kampe & Arlettaz 2009), which limits conclusions about species' habitat preferences and species-specific habitat restoration actions. Even in our study population, a previous study has focused on habitat selection of male hoopoes only and showed an optimum of 60-80% bare ground at the foraging scale (Schaub *et al.* 2010; Tagmann-loset *et al.* 2012). Our study now

provides additional important information about the foraging differences between the sexes, which should help formulating clearer management recommendations.

Here we demonstrate sex-specific foraging niches and the preferences for certain parcel characteristics during a brood stage, where size differences between the chicks are large and where different prey sizes are needed. That asynchronous breeding will lead to adaptations in feeding behavior has already been demonstrated in the pied flycatcher, where female birds brought smaller prey at younger but not older nestling stages (Wiebe & Slagsvold 2009). Such feeding rules could be plastic and adjusted to the degree of asynchrony and the age of the chicks. Sex-specific differences in habitat use could be large when chicks differ in size, but vanish as soon as all nestling are big enough to feed on large prey. Alternatively, sex-specific foraging preferences could persist throughout the annual cycle not being restricted to a certain period during the breeding stage (Selander 1966; Radford & Du Plessis 2003; Stenberg & Hogstad 2004). In hoopoes bill morphology shows the highest sexual dimorphism compared to other morphological traits (Glutz von Blotzheim & Bauer 1980), indicating that males and females may intrinsically differ in their foraging behavior with the concomitant consequences on variation in habitat preferences. Future studies investigating the plasticity of male and female feeding behavior are clearly needed, in order to better understand the evolution of sex-specific resource exploitation patterns and their consequences on habitat use.

#### Acknowledgements

Special thanks to my supervisors Alain Jacot and Raphaël Arlettaz for the support during the project from development till writing the thesis. Thanks to all my helpers in the field and office: Valentin Moser, Jasmin Knutti, Barbara Hildebrand, Lara Moreno, Michaela Föhn, Laura Bosco, Debora Unternährer, Arnaud Barras, Urs Kormann and Claire Guyot. Further I like to thank the Vogelwarte Sempach, especially Jérôme Duplain for their support with material and knowledge. Last but not least I like to thank all the farmers involved, who let me take out my field-work on their property.

### Tables

 Table 1: Variables recorded on presence and pseudo-absence parcels for female birds

 Female

rem				
No.	Variable	Presence parcels	Pseudo-absence parcels	
	-	11-44	11-44	
	Ground cover variables (%)	Media	an ± MAD	
1	Vegetation middle row	80.5 ± 17.8	70 ± 27.8	
2	Bare ground middle row	7.5 ± 7.4	7.5 ± 11.1	
3	Litter middle row	$10 \pm 10.7$	$10.8 \pm 15$	
4	Vegetation under trees	21.3 ± 27.8	6.3 ± 9.3	
5	Bare ground under trees	45 ± 23	60 ± 29.7	
6	Litter under trees	18.8 ± 16.7	17.5 ± 14.8	
	Vegetation variables	Media	an ± MAD	
7	Mean vegetation height middle row	7.8 ± 3.3	7.9 ± 4.8	
8	Mean vegetation height under trees	5.5 ± 5.7	4 ± 5.9	
9	Mean plantation-tree height	3 ± 0.7	3 ± 0.7	
	Invertebrate variables	Median ± MAD		
10	Invertebrate abundance	91.3 ± 33.4	90 ± 29.7	
11	Shannon diversity index	1.7 ± 0.1	$1.5 \pm 0.3$	
		Mear	n / Range	
12	– Invertebrate richness	8.8 / 12	8.1 / 12	
13	Insect richness	4.5 / 7	4.3 / 7	
14	Plantation type	No. of o	bservations	
	Apple	29	24	
	Pear	4	15	
	Apricot	10	5	
	Others	1	0	

Male	2			
No.	Variable	Presence parcels n=46	Pseudo-absence parcels n=46	
	– Ground cover variables (%)	Medi	an ± MAD	
1	Vegetation middle row	78.8 ± 16.7	75 ± 25.2	
2	Bare ground middle row	9.5 ± 9.6	6.75 ± 10	
3	Litter middle row	$10 \pm 11.1$	$10.8 \pm 14.5$	
4	Vegetation under trees	5.5 ± 8.2	9.3 ± 13.7	
5	Bare ground under trees	66.3 ± 24.1	63.8 ± 31.5	
6	Litter under trees	17.5 ± 14.8	16.8 ± 17.4	
	Vegetation variables	Median ± MAD		
7	Mean vegetation height middle row	8.3 ± 3.7	8.8 ± 4.1	
8	Mean vegetation height under trees	3.1 ± 4.6	$4.6 \pm 6.9$	
9	Mean plantation-tree height	3 ± 0.7	3 ± 0.7	
	Invertebrate variables	Median ± MAD		
10	Invertebrate abundance	94.5 ± 29.7	81.3 ± 39.7	
11	Shannon diversity index	1.7 ± 0.2	$1.6 \pm 0.2$	
		Mea	n / Range	
12	Invertebrate richness	9 / 12	8 / 12	
13	Insect richness	5 / 7	4 / 7	
14	Plantation type (categorical)	No. of observations		
	Apple	28	29	
	Pear	6	10	
	Apricot	10	7	
	Others	2	0	

VENO.		r type is cu	cegorical its	presence ii	i u mouer i		ien a		
Male									
Rank	Intercept	BA	TR	IN	IRI	Deviance	df	ΔAICc	AICc weight
1	-2.94e <sup>-3</sup>	0.	37	0.44		121.5	5	0.00	0.23
2	9.6e <sup>-4</sup>			0.	39	124.2	4	0.55	0.17
3						127.5	3	1.66	0.10
4	-1.29e <sup>-3</sup>	0.	31			125.5	4	1.74	0.09
Femal	e								
Rank	Intercept	SHIN	PLTY	LIRO	VERO	Deviance	df	ΔAICc	AICc weight
1	-5.88	3.77	+	-0.43		99.1	8	0.00	0.15
2	-5.27	3.40	+		0.40	99.4	8	0.40	0.12
3	-5.49	3.55	+			101.2	7	0.58	0.11
4	-6.09	3.81		-0.46		107	5	0.80	0.10
5	-5.64	3.62	+	-0.31	0.24	98.3	9	1.74	0.06
6	-5.54	3.48			0.38	108.1	5	1.97	0.06

**Table 3:** Ranking of the GLMMs with  $\Delta$ AlCc<2 from first ranked. The models include parcel and individual as random effect. Fixed effects are: Bare ground under trees; BATR, Insect richness; INRI, Litter middle row; LIRO, Shannon diversity index; SHIN, Plantation type; PLTY, Vegetation middle row; VERO. As plantation type is categorical its presence in a model is indicated with a + sign.

**Table 4:** Model outputs of testing whether Arthropod richness, Arthropod abundance, Shannon index and Insect richness differ between plantation types. P-values lower than 0.05 are represented in bold.

		Plantation type				
		Apple	Pear	Others		
			Arthropod richnes	5		
		-0.46±0.2	-0.28±0.24	0.04±0.6		
	Apricot	t <sub>176</sub> =-2.3	t <sub>176</sub> =-1.2	t <sub>176</sub> =0.1		
		p=0.02	p=0.25	p=0.94		
			0.18±0.19	0.50±0.58		
	Apple		t <sub>176</sub> =0.93	t <sub>176</sub> =0.86		
			p=0.36	p=0.39		
				0.32±0.6		
	Pear			t <sub>176</sub> =0.54		
				p=0.59		
		Ai	rthropod abundan	ce		
		-0.42±0.2	-0.22±0.24	-0.37±0.6		
	Apricot	t <sub>176</sub> =-2.11	t <sub>176</sub> =-0.9	t <sub>176</sub> =-0.62		
		p=0.04	p=0.37	p=0.53		
			0.2±0.19	0.05±0.58		
	Apple		t <sub>176</sub> =1.05	t <sub>176</sub> =0.08		
			p=0.29	p=0.93		
	Pear			-0.16±0.6		
				t <sub>176</sub> =-0.26		
				p=0.8		
Reference plantation type		Shannon index				
		0.003±0.04	-0.03±0.05	-0.004±0.13		
	Apricot	t <sub>176</sub> =0.08	t <sub>176</sub> =-0.6	t <sub>176</sub> =-0.03		
		p=0.93	p=0.54	p=0.97		
			-0.04±0.04	-0.008±0.12		
	Apple		t <sub>176</sub> =-0.86	t <sub>176</sub> =-0.06		
			p=0.39	p=0.95		
	_			0.03±0.13		
	Pear			t <sub>176</sub> =0.21		
				p=0.83		
			Insect richness			
		-0.34±0.2	-0.14±0.24	0.68±0.6		
	Apricot	t <sub>176</sub> =-1.7	t <sub>176</sub> =-0.59	t <sub>176</sub> =1.13		
		p=0.09	p=0.56	p=0.26		
			0.2±0.2	1.02±0.58		
	Apple		t <sub>176</sub> =1.02	t <sub>176</sub> =1.75		
			p=0.31	p=0.08		
				0.82±0.6		
	Pear			t <sub>176</sub> =1.38		
				p=0.17		

#### Legend captions

Figure 1: Occurrence probability of female hoopoe plotted against Shannon diversity index for (a) apricot, (b) apple and (c) pear plantations. Solid lines indicating model predictions with corresponding 95% CI's in grey, while raw data are jittered around 0 (=pseudo-absence parcels) and 1 (=presence parcels). Occurrence probabilities greater than 0.5 indicate selection or preference, whereas values lower than 0.5 should be interpreted as avoidance, relative to the other available habitats (Beyer *et al.* 2010).

Figure 2: Occurrence probability of male hoopoe plotted against insect richness. Solid line indicating model prediction with corresponding 95% CI in grey, while raw data are jittered around 0 (=pseudo-absence parcels) and 1 (=presence parcels). Occurrence probabilities greater than 0.5 indicate selection or preference, whereas values lower than 0.5 should be interpreted as avoidance, relative to the other available habitats (Beyer *et al.* 2010).

Figure 3: Occurrence probability of male hoopoe plotted against proportion of bare ground under the trees. Solid line indicating model prediction with corresponding 95% CI in grey, while raw data are jittered around 0 (=pseudo-absence parcels) and 1 (=presence parcels). Occurrence probabilities greater than 0.5 indicate selection or preference, whereas values lower than 0.5 should be interpreted as avoidance, relative to the other available habitats (Beyer *et al.* 2010).

Figure 4: Mean bout distance to nest in meter of the two sexes on log scale, blue line indicates predicted value and the grey area its 95% confidence interval. Dots reflect raw data of each foraging bout.









Figure 2



Figure 3:



Figure 4:



sex

### References

- Arlettaz, R., Schaad, M., Reichlin, T.S. & Schaub, M. (2010a) Impact of weather and climate variation on hoopoe reproductive ecology and population growth. *Journal of Ornithology*, **151**, 889-899.
- Arlettaz, R., Schaub, M., Fournier, J., Reichlin, T.S., Sierro, A., Watson, J.E.M. & Braunisch, V. (2010b)
   From publications to public actions: When conservation biologists bridge the gap between
   research and implementation. *BioScience*, 60, 835-842.
- Barbaro, L., Couzi, L., Bretagnolle, V., Nezan, J. & Vetillard, F. (2008) Multi-scale habitat selection and foraging ecology of the Eurasian hoopoe (Upupa epops) in pine plantations. *Biodiversity and Conservation*, **17**, 1073-1087.
- Bartoń, K. (2016) MuMIn: Multi-model inference. R package version 1.15.6, https://cran.r-project.org/web/packages/MuMIn/index.html.
- Bates, D., Machler, M., Bolker, B.M. & Walker, S.C. (2015) Fitting linear mixed-effects models using Ime4. *Journal of Statistical Software*, **67**, 1-48.
- Baur, B., Baur, H., Roesti, C. & Roesti, D. (2006) *Die Heuschrecken der Schweiz*. Haupt Verlag, Bern.
- Beck, C.A., Iverson, S.J. & Bowen, W.D. (2005) Blubber fatty acids of gray seals reveal sex differences in the diet of a size-dimorphic marine carnivore. *Canadian Journal of Zoology*, **83**, 377-388.
- Beyer, H.L., Haydon, D.T., Morales, J.M., Frair, J.L., Hebblewhite, M., Mitchell, M. & Matthiopoulos, J.
   (2010) The interpretation of habitat preference metrics under use-availability designs.
   *Philosophical Transactions of the Royal Society B, Biological Sciences*, 365, 2245-2254.
- Bravo, C., Ponce, C., Bautista, L.M. & Alonso, J.C. (2016) Dietary divergence in the most sexually sizedimorphic bird. *The Auk*, **133**, 178-197.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference,* Second edn. Springer-Verlag, New York.
- Calenge, C. (2006) The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, **197**, 516-519.
- Calenge, C. (2007) Exploring habitat selection by wildlife with adehabitat. *Journal of Statistical Software*, **22**, 1-19.
- Catry, T., Alves, J.A., Gill, J.A., Gunnarsson, T.G. & Granadeiro, J.P. (2012) Sex promotes spatial and dietary segregation in a migratory shorebird during the non-breeding season. *PLoS ONE*, **7**, e33811.
- Class, A.M. & Moore, I.T. (2013) Effects of food supplementation on a tropical bird. *Oecologia*, **173**, 355-362.
- Cramp, S.ed. (1985) Volume IV: Terns to Woodpeckers. *Handbook of the birds of Europe, the Middle East and North Africa: The birds of the Western Palearctic*, pp. 786-799. Oxford University Press, Oxford.
- Fournier, J. & Arlettaz, R. (2001) Food provision to nestlings in the hoopoe (*Upupa epops*): implications for the conservation of a small endangered population in the Swiss Alps. *Ibis*, **143**, 2-10.
- Gasparini, J., Roulin, A., Gill, V.A., Hatch, S.A. & Boulinier, T. (2006) In kittiwakes food availability partially explains the seasonal decline in humoral immunocompetence. *Functional Ecology*, **20**, 457-463.
- Gelman, A., Su, Y.-S., Yajima, M., Hill, J., Grazia Pittau, M., Kerman, J., Zheng, T. & Dorie, V. (2015) arm: Data analysis using regression and multilevel/hierarchical models. R package version 1.8-6, https://cran.r-project.org/web/packages/arm/index.html.
- Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, J.L., Saher, D.J., Stevens, C.E. & Jerde, C.L. (2006) Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, **75**, 887-898.
- Glutz von Blotzheim, U.N. & Bauer, K.M. (1980) *Upupa epops* Linnaeus 1758 Wiedehopf. *Handbuch der Vögel Mitteleuropas* (ed. U.N. Glutz von Blotzheim), pp. 852-876. Akademische Verlagsgesellschaft, Wiesbaden.

- Guillod, N., Arlettaz, R. & Jacot, A. (2016a) Impact of spatial variation of crucial prey, the molecricket, on hoopoe territory occupancy and reproduction. *Journal of Avian Biology*, doi: 10.1111/jav.00990.
- Guillod, N., Arlettaz, R. & Jacot, A. (2016b) Impact of spatial variation of crucial prey, the molecricket, on hoopoe territory occupancy and reproduction. *Journal of Avian Biology,* **doi: 10.1111/jav.00990**.
- Hijmans, R.J., van Etten, J., Mattiuzzi, M., Sumner, M., Greenberg, J.A., Perpinan Lamigueiro, O.,
   Bevan, A., Racine, E.B. & Shortridge, A. (2015) raster: Geographic data analysis and modeling.
   R package version 2.5-2, https://cran.r-project.org/web/packages/raster/index.html.
- Hosmer, D.W., Jr. & Lemeshow, S. (1989) Applied logistic regression. John Wiley & Sons, New York.
- Houston, D. & Shine, R. (1993) Sexual dimorphism and niche divergence: feeding habits of the Arafura filesnake. *Journal of Animal Ecology*, **62**, 737-748.
- Le V. dit Durell, S.E.A., Goss-Custard, J.D. & Caldow, R.W.G. (1993) Sex-related differences in diet and feeding method in the oystercatcher *Haematopus ostralegus*. *Journal of Animal Ecology*, **62**, 205-215.
- Martín-Vivaldi, M., Palomino, J.J., Soler, M. & Soler, J.J. (1999) Determinants of reproductive success in the hoopoe *Upupa epops*, a hole-nesting non-passerine bird with asynchronous hatching. *Bird Study*, **46**, 205-216.
- Menz, M.H.M., Mosimann-Kampe, P. & Arlettaz, R. (2009) Foraging habitat selection in the last ortolan bunting *Emberiza hortulana* population in Switzerland: final lessons before extinction. *Ardea*, **97**, 323–333.
- Morris, E.K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T.S., Meiners, T., Müller, C.,
   Obermaier, E., Prati, D., Socher, S.A., Sonnemann, I., Wäschke, N., Wubet, T., Wurst, S. &
   Rillig, M.C. (2014) Choosing and using diversity indices: insights for ecological applications
   from the German biodiversity exploratories. *Ecology and Evolution*, 4, 3514-3524.
- Nagendra, H. (2002) Opposite trends in response for the Shannon and Simpson indices of landscape diversity. *Applied Geography*, **22**, 175-186.
- Pekár, S., Martišová, M. & Bilde, T. (2011) Intersexual trophic niche partitioning in an ant-eating spider (Araneae: Zodariidae). *PLoS ONE*, **6**, e14603.
- Perry, G. (1996) The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguania): evidence from intraspecific variation in foraging behavior and diet. *Canadian Journal of Zoology*, **74**, 1238-1245.
- Pinheiro, N., Bates, D., DebRoy, S., Sarkar, D. & R. Development Core Team (2012) nlme: linear and nonlinear mixed effects models. R package version 3.1-111, https://cran.r-project.org/web/packages/nlme/index.html.
- QGIS Development Team (2015) QGIS Geographic information system. Open Source Geospacial Foundation Project, Version 2.10.1, http://www.qgis.org/.
- R Development Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Version 3.3.1, https://www.r-project.org/.
- Radford, A.N. & Du Plessis, M.A. (2003) Bill dimorphism and foraging niche partitioning in the green woodhoopoe. *Journal of Animal Ecology*, **72**, 258-269.
- Ricklefs, R.E. & Miller, G.L. (1999) Ecology, 4 edn. W.H. Freeman, New York.
- Ryan, P.G., Petersen, S.L., Peters, G. & Grémillet, D. (2004) GPS tracking a marine predator: the effects of precision, resolution and sampling rate on foraging tracks of African Penguins. *Marine Biology*, **145**, 215-223.
- Ryser, S., Guillod, N., Bottini, C., Arlettaz, R. & Jacot, A. (2016) Sex-specific food provisioning patterns by parents in the asynchronously hatching European hoopoe. *Animal Behaviour*, **117**, 15-20.
- Schaub, M., Martinez, N., Tagmann-Ioset, A., Weisshaupt, N., Maurer, M.L., Reichlin, T.S., Abadi, F.,
   Zbinden, N., Jenni, L. & Arlettaz, R. (2010) Patches of bare ground as a staple commodity for
   declining ground-foraging insectivorous farmland birds. *PLoS ONE*, 5, e13115.
- Selander, R.K. (1966) Sexual dimorphism and differential niche utilization in birds. *The Condor*, **68**, 113-151.

- Shine, R. (1989) Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *The Quarterly Review of Biology*, **64**, 419-461.
- Slagsvold, T. & Sonerud, G.A. (2007) Prey size and ingestion rates in raptors: importance for sex roles and reversed sexual size dimorphism. *Journal of Avian Biology*, **38**, 650-661.
- Stenberg, I. & Hogstad, O. (2004) Sexual dimorphism in relation to winter foraging in the whitebacked woodpecker (*Dendrocopos leucotos*). *Journal of Ornithology*, **145**, 321-326.
- Stenning, M.J. (1996) Hatching asynchrony, brood reduction and other rapidly reproducing hypotheses. *Trends in Ecology & Evolution*, **11**, 243-246.
- Stephens, D.W. & Krebs, J.R. (1986) Foraging Theory. Princeton University Press, Princeton.
- Tagmann-Ioset, A., Schaub, M., Reichlin, T.S., Weisshaupt, N. & Arlettaz, R. (2012) Bare ground as a crucial habitat feature for a rare terrestrially foraging farmland bird of Central Europe. *Acta Oecologica*, **39**, 25-32.
- Temeles, E.J., Miller, J.S. & Rifkin, J.L. (2010) Evolution of sexual dimorphism in bill size and shape of hermit hummingbirds (Phaethornithinae): a role for ecological causation. *Philosophical Transactions of the Royal Society B, Biological Sciences*, **365**, 1053-1063.
- Tschumi, M., Schaub, M. & Arlettaz, R. (2014) Territory occupancy and parental quality as proxies for spatial prioritization of conservation areas. *PloS ONE*, **9**, e97679.
- Webster, M.S. (1997) Extreme sexual size dimorphism, sexual selection, and the foraging ecology of Montezuma oropendolas. *The Auk*, **114**, 570-580.
- Wickham, H. (2011) The split-apply-combine strategy for data analysis. *Journal of Statistical Software*, **40**, 1-29.
- Wiebe, K.L. & Slagsvold, T. (2009) Parental sex differences in food allocation to junior brood members as mediated by prey size. *Ethology*, **115**, 49-58.

### Appendix

Territory Nr.	Sex	Parcel No.	Туре	Coordinates (WGS 84: lat/lon)	
		1	Р	46.12430, 7.10457	
		1	А	46.12471, 7.10327	
	2	2	Р	46.12465, 7.10536	
	T	2	А	46.12484, 7.10585	
		3	А	46.12628, 7.10350	
A12		1	Р	46.12430, 7.10457	
AIZ		I	А	46.12471, 7.10327	
		2	Р	46.12465, 7.10536	
	m	Σ	А	46.12484, 7.10585	
		3	Р	46.12551, 7.10457	
			А	46.12628, 7.10350	
		4	Р	46.12516, 7.10397	
		7	A	46.12572, 7.10259	
		1	Р	46.12674, 7.10889	
			A	46.12569, 7.10959	
		2	Р	46.12716, 7.11386	
	f		A	46.12628, 7.11272	
	•	3	Р	46.12892, 7.11262	
			A	46.12915, 7.11290	
		4	Р	46.12868, 7.10978	
—		•	A	46.12799, 7.11089	
A18		1	Р	46.12818, 7.11368	
			A	46.12881, 7.11231	
		2	Р	46.12932, 7.11554	
			А	46.13033, 7.11490	
	m	3	Р	46.12947, 7.11581	
			А	46.12975, 7.11623	
			Р	46 12869 7 11659	
		4	Δ.	46 12848 7 11632	
			D D	46 14521 7 12541	
			1	Γ	40.14521, 7.15541
			P	46 14563 7 13484	
		2	A	46 14609 7 13403	
	f		P	46 14539 7 13456	
		3	A	46.14505, 7.13331	
			P	46 14519 7 13432	
		4	A	46.14459. 7.13380	
A42 —			P	46.14772, 7.13222	
		1	A	46.14783. 7.13254	
			Р	46.14391, 7.13061	
	m	2	A	46.14345. 7.13154	
		3	Р	46.14274. 7.13183	
			А	46.14259, 7.13314	
		4	Р	46.14504, 7.13643	
			А	46.14397, 7.13719	

Appendix-Table 1: GPS Coordinates of all parcels sampled during the project:

		1	Р	46.14827, 7.13883
			А	46.14784, 7.13901
		n	Р	46.14695, 7.13694
A 4 7	f	2	А	46.14739, 7.13645
A47	I	2	Р	46.14704, 7.14216
			А	46.14711, 7.14161
		Л	Р	46.14803, 7.14214
		<b>T</b>	A	46.14787, 7.14293
		1	Р	46.16633, 7.17117
			A	46.16630, 7.17239
		2	Р	46.16564, 7.17132
	f	<u>۲</u>	A	46.16580, 7.17186
	I I	3	Р	46.16490, 7.16905
			Α	46.16503, 7.17132
		Л	Р	46.16432, 7.16948
A68 -		4	А	46.16402, 7.16868
A08		1	Р	46.16582, 7.17014
		1	А	46.16648, 7.16972
		2	Р	46.16525, 7.17193
	~	Ζ	А	46.16546, 7.17263
	111	3	Р	46.16352, 7.17050
			А	46.16242, 7.17136
		4	Р	46.16295, 7.16886
			А	46.16202, 7.16981
		1	Р	46.11699, 7.11806
			А	46.11824, 7.11891
		2	Р	46.11797, 7.11616
	f	2	А	46.11833, 7.11729
	I	2	Р	46.11426, 7.11619
		5	А	46.11451, 7.11668
		Λ	Р	46.11579, 7.12098
100		4	А	46.11532, 7.12048
A96		1	Р	46.11667, 7.11741
		T	А	46.11682, 7.11731
		2	Р	46.11552, 7.11866
		Z	А	46.11519, 7.11844
		3	Р	46.11410, 7.11518
			А	46.11444, 7.11495
		4	Р	46.11668, 7.12200
			А	46.11699, 7.12072

			P	46 12354 7 12412
		1	A	46.12330, 7.12412
		2	P	46 12434 7 12522
			A	46.12409. 7.12576
	f		P	46 12325 7 12634
	•	3	Δ	46 12294 7 12493
			P	46.12294,7.12435
		4	A	46 12211 7 12513
A101			P	46 12312 7 12439
		1	A	46 12258 7 12291
			P	46 12349 7 12410
		2	A	46 12296 7 12267
	m		P	46 11943 7 12213
		3	Δ	46 12012 7 12166
			P	46 11995 7 12344
		4	Δ	46 12012 7 12332
			P	46 15773 7 20190
		1	Δ	46 15707 7 20282
			P	46.15553 7.20158
		2	Δ	46.15584 7.20136
	f		P A	40.15384, 7.20270
		3	F A	40.15792, 7.19931
			A B	40.13772, 7.19882
		4	P	40.15549, 7.19080
A128			A D	40.13030, 7.19333
		1	F	40.13470, 7.19744
		2	A	40.13431, 7.13873
			F	40.13402, 7.13700
	m	3	A B	40.13390, 7.19773
			P	40.10117, 7.20300
			A B	40.10155, 7.20554
		4	P	40.10042, 7.20372
			A	40.10001, 7.20410
		1	P	40.19650, 7.27671
			A B	40.19897, 7.27381
	f	2	P	40.19940, 7.20981
			<u>A</u>	46.19911, 7.26869
		3	P	46.19865, 7.26981
			<u>A</u>	46.19887, 7.27036
B9		1	P	46.19787, 7.27315
			A	46.19811, 7.27369
		2	P	46.19764, 7.27267
	m	_	A	46.19698, 7.27354
		3	Р	46.19667, 7.27274
			A	46.19640, 7.27211
		4	Р	46.19808, 7.27110
			А	46.19792, 7.27054

		1	Р	46.19704, 7.26119
			А	46.19658, 7.26040
		2	Р	46.19749, 7.26197
			А	46.19827, 7.26296
	t		Р	46.19556, 7.26321
		3	А	46.19515. 7.26421
B17			Р	46.19626, 7.26357
		4	A	46.19634. 7.26420
			Р	46.19334, 7.25992
		1	A	46 19285 7 26086
	m		P	46.19394. 7.26149
		2	A	46.19521, 7.26041
			P	46 16722 7 20507
		1	A	46 16736 7 20388
			P	46 16632 7 20372
		2	A	46.16669. 7.20372
B40	m		P	46 16559 7 20199
		3	A	46 16646 7 20084
			P	46 16614 7 20220
		4	Δ	46.16677 7.20220
			P	46.18617, 7.25225
		1	Δ	46.18599 7.25191
			P	46.18792 7.25058
		2	Δ	46 18739 7 25163
	f		D D	46.19801 7.25165
		3	Δ	46 19820 7 26588
		4	P	46.19298 7.26297
			Δ	46 19255 7 26374
B42			P	46.19758 7.26197
		1	Δ	46 19785 7 26085
		2	P	46.19752, 7.25490
			Δ	46.19291 7.25426
	m	3	P	46.18135 7.24462
			Δ	46 18114 7 24391
			P	46 18148 7 24586
		4	A	46 18133 7 24629
			<u>Р</u>	46 25105 7 43049
		1	A	46 25060 7 43147
			P	46 25063 7 43026
		2	Δ	46.25020, 7.43020
	f		 D	46.25020, 7.43125
		3	^	46.25326, 7.42556
			D	46.25305, 7.42801
		4	F A	40.25200, 7.42782
D7			A	40.23201, 7.42727
		1	۲ ۸	40.23273, 7.43102
			A	40.23270, 7.43204
		2	۲	40.20190, /.4290/
	m		<u>A</u>	40.201/3, /.42910
		3	۲ ۲	40.20204, 7.42908
			<u>A</u>	40.25230, 7.42821
		4	۰ ۲	40.25289, /.42642
			A	46.25249, 7.42654

Appendix-Figure 1: Graphical representation of the home range (95 % density estimation) of the 10 bird pairs. Male birds are represented in blue, females in red. Territory number indicated on top of every graph.





## **Declaration of consent**

On the basis of Article 28 para. 2 of the RSL05 phil.-nat

Name/First Name:	Bühler Roman Heinrich				
Matriculation number: 10-414-100					
Study program: Master of Science in Ecology and Evolutio					
	Bachelor 🗌	Master	Dissertation		
Title of the thesis:	Sex-specific foraging ni	ches and habitat selec	ction in an asynchronously		
	breeding bird, the Euro	pean hoopoe <i>Upupa</i> e	epops		
Supervisors:	Dr. Alain Jacot, Prof. Dr	. Raphaël Arlettaz			

I declare herewith that this thesis is my own work and that I have not used any sources other than those stated. I have indicated the adoption of quotations as well as thoughts taken from other authors as such in the thesis. I am aware that the Senate pursuant to Article 36 para. 1 lit. r of the University Act of 5 September, 1996 is authorized to revoke the title awarded on the basis of this thesis. I allow herewith inspection in this thesis.

Place/Date

Signature

Bern, 15.09.2016