

**Landscape of prey in a hoopoe population:
consequences of spatial variation of molecricquet
availability on reproductive success and
conservation strategies**

**Masterarbeit der Philosophisch-naturwissenschaftlichen Fakultät
der**

Universität Bern

vorgelegt von

Nicolas Guillod

2013

Leiter der Arbeit

Prof. R. Arlettaz

Dr. A. Jacot

1. Abstract

Individual fitness and population persistence is mainly determined by direct benefits accrued from securing a territory of sufficient quality. Food supply is one of the main determinants of territory quality, with spatial and temporal variation in prey availability largely dictating reproductive output and thus population dynamics. In a Swiss hoopoe *Upupa epops* population, molecrickets *Gryllotalpa gryllotalpa*, the most profitable prey locally, make up a huge fraction of the prey biomass delivered to chicks by parents, but there is considerable variation among broods. We investigated the impact of molecricket prey on hoopoes' fitness-related traits by quantifying the spatial variation in the food allocation pattern of parents to chicks across the whole population range and analysed the impact of this prey on past and current reproduction. We found a considerable spatial variation of molecricket biomass in the diet provisioned to chicks across the whole population range, and the pattern was spatially very consistent from year to year over 11 years, which indicates the existence of prey hotspots. This spatial heterogeneity in staple prey supply is mirrored both in the history of territory occupancy (2002-2011) and in present-day reproductive success (2012). It also affects chick physiological state and reproduction: higher the proportion of molecrickets in chicks' diet, better their body condition, and higher hatching and fledging rates. This study highlights the impact of a single, extremely profitable prey species on parents' provisioning strategy and, ultimately, on overall reproductive success.

Keywords

Food allocation; reproduction; spatial variation; territory quality; territory occupancy

Table of contents

1.	Abstract.....	2
2.	Introduction	4
3.	Material & Methods.....	6
3.1.	Study area and species	6
3.2.	Parental food provisioning.....	8
3.3.	Analysis of film material.....	9
3.4.	Spatially-explicit visualization of prey "availability"	10
3.5.	Statistical analysis	10
4.	Results.....	12
4.1.	Repeatability of dietary composition across space and time.....	12
4.2.	Feeding pattern.....	12
4.2.1.	Prey biomass.....	12
4.2.2.	Daily rhythms in chick provisioning	13
4.3.	Fitness-related traits	13
4.3.1.	The effects of molecricket "availability" on occupancy rate.....	13
4.3.2.	The effect of molecrickets on current reproductive success	14
5.	Discussion	14
6.	References	19
7.	Acknowledgements	22
8.	Figure legends	23
9.	Figures.....	24
10.	Appendix.....	28

2. Introduction

Variation in food distribution and, especially, availability are critical factors influencing the breeding performance of birds. Food availability varies in time and space, with species responding to this environmental uncertainty by trying to select high-quality territories and by timing reproduction with peaks in prey abundance (Martin 1987; Van Noordwijk, McCleery, & Perrins 1995). However, not all individuals have access to high quality territories. Instead, some must settle in suboptimal if not poor territories. There is thus often a despotic distribution of phenotypes across the landscape (Tschumi *et al.* in prep.), which is mirrored in the reproductive output, both past and present, achieved in a given territory (Sergio & Newton 2003; Tremblay *et al.* 2003; Catry, Franco, & Sutherland 2012). Prey is hardly ever available at discretion: as a main limiting environmental factor, in particular during the highly demanding reproductive phase, it actually is the basic cause of intraspecific competition, i.e. what generates a despotic spatial distribution of phenotypes (Fretwell & Lucas 1969; Orians & Wittenberger 1991). Spatial variation in breeding habitat use is hence largely influenced by the phenology, physiology and the habitat associations and ecological requirements of the prey itself. Although there are many experimental studies that have manipulated both food availability (e.g., (Simons & Martin 1990; Orians & Wittenberger 1991; Richner 1992)) and brood size (Perrins 1964; Hegner & Wingfield 1987; Korpimaki 1988), only a handful of studies have focused on the effects of naturally occurring spatial variation of food availability on the short- and long-term reproductive performance and population dynamics of animal species (e.g. Ens *et al.* 1995; Valkama *et al.* 2002).

Several studies have established a link between habitat/territory quality and annual reproductive output (e.g. Lambrechts *et al.* 2004; Bruinzeel, Pol, & Trierweiler 2005; Valcu & Kempenaers 2008), but it mostly remains elusive which underlying factors operate. While weather-protected and predation-free nesting sites appear to be crucial (Williams, Plessis, & Siegfried 1991), prey availability is likely to play an as important if not greater role (Martin 1987). In blue tits, for instance, a comparison across different types of breeding habitat revealed that caterpillar abundance is the main determinant of traits related to reproduction, such as the timing of egg laying, clutch size, chick growth and development, and nestling survival (Perrins 1965; Tremblay *et al.* 2003). The same applies to homogeneous habitats: in lesser kestrels *Falco naumanni*, colonies that feed high amounts of molecrickets show a higher reproductive performance (Catry, Franco, & Sutherland 2012). A similar pattern has been observed in another molecricket specialist, the hoopoe. Its breeding success depends not only on the overall biomass provisioned to chicks (Martín-vivaldi *et al.* 1999; Arlettaz *et al.* 2010a), but most likely also on the proportion of molecrickets entering chicks' diet (Arlettaz, Fournier, & Zbinden 2000; Fournier & Arlettaz 2001). General prey availability and even the availability of a single prey species may thus govern individual reproductive success and, ultimately, the persistence of a bird population.

Defining prey availability, which is abundance modified by accessibility, remains a real challenge, especially in predators-prey investigations that are carried out on wide areas. It is nevertheless essential to understand the spatial patterns of prey availability, notably for prioritizing conservation effort across the landscape. The number of times a territory has been successfully occupied over a time period can be used as a proxy of territory quality (Sergio & Newton 2003). If the

species shows a high degree of trophic specialization, as lesser kestrels and hoopoes do, territory occupancy could thus indirectly inform about the spatial availability of a staple food resource, without the necessity to measure both prey abundance and its accessibility. In effect, the latter is especially difficult to quantify because it requires that one measures prey accessibility from a predator's perspective, while we mostly ignore how a predator perceives its prey and acquires its food. Based on the observation that molecrickets are likely to exert some selective pressure on hoopoes in a small Swiss Alpine population (Arlettaz, Fournier, & Zbinden 2000; Fournier & Arlettaz 2001; Arlettaz *et al.* 2010a), we investigated, at population range scale, the relationships between territory occupancy (which varies locally, see Tschumi *et al.* in prep.) and reproductive success vs. molecricket biomass provisioned to chicks by parents. We so hope to provide practitioners with both spatially-explicit recommendations for prioritizing areas for the conservation of this local hoopoe population and guidance for the conservation of other hoopoe populations that rely on molecrickets.

3. Material & Methods

3.1. Study area and species

The study was carried out on the plain of the upper Rhone valley, in the southwestern Swiss Alps (Valais, Switzerland; 46°07'N, 07°08'N) between Vernayaz and Leuk. The whole study area has an extension of ca. 70 km² and is characterized by high-intensity agriculture, dominated by fruit tree plantations and vegetable crops. The Eurasian hoopoe is an endangered, migratory species in Switzerland (Bächler *et al.* 2010) with an estimated breeding population of 190-230 pairs (Schweizerische Vogelwarte, Sempach). In the past, the Swiss

population was much larger and occupied a much wider range, but its stronghold has always been in Valais (Arlettaz *et al.* 2010b). The Valais population itself reached very low levels in the 1980s, which called for a targeted conservation research project (Fournier & Arlettaz 2001) that identified a lack of suitable breeding sites close to the main molecricicket-rich foraging grounds on the plain as a critical factor. Hundreds of nestboxes were therefore installed in agricultural sheds and buildings since 1999, which led to a dramatic increase of the population of this secondary cavity breeder within a few years only (Arlettaz *et al.* 2010b). The whole population has been monitored continuously since then, with comprehensive information about nestbox occupancy, allowing quantifying territory quality, and about breeding parameters (clutch size, number of hatchlings and fledglings) and morphometric traits (body mass, tarsus length, wing length, measured at day 18 after hatching). Like many other terrestrially foraging insectivorous birds (Schaub *et al.* 2010), hoopoes need patches of bare soil on their feeding grounds for accessing their ground-dwelling and, especially, underground-dwelling prey, as demonstrated in studies carried out in our study population (Tagmann-Ioset *et al.* 2012). Molecricickets furthermore occur patchily within the study area, having specific habitat requirements (Tagmann-Ioset *et al.* 2012), but Tschumi *et al.* (in prep.) were not able to link hoopoe breeding success to molecricicket distribution across the landscape, which might be due to unreliable methods to assess molecricicket availability for hoopoe (abundance was estimated through the presence of underground galleries and accessibility through measures of soil hardness and ground vegetation structure).

3.2. *Parental food provisioning*

Sex-specific parental food provisioning behaviour was recorded at days 11-15 after hatching, which corresponds to the period when the female stops warming the young – which now thermoregulate by themselves – and starts provisioning prey, assisting the male in this intensive task. Beforehand, the male passes the prey items singly to the female that feeds the chicks. Adults were ring-marked in colour for identification on the video footage, with in some cases additional marking made on a few head feathers with a blue acryl marker, this to facilitating proper identification of the adults. Food delivery was filmed during 24 h in a row with small infrared cameras (Conrad, platin camera 8.47 mm, CCD S/W-camera, resolution 297'984 pixels, optical resolution of 512 x 582 pixels; and Conrad, platin camera, Sharp CCD colour camera, resolution of 437'664 pixels, optical resolution 752 x 582 pixels with wide-angle lenses (Conrad lens 3.6 mm)) and recorders (Lupus AEON-MDVR Mini Security Recorder) equipped with 4 GB SD memory cards. Both devices had power supplied by two car batteries (Panasonic 6V rechargeable sealed lead-acid battery) connected via converter cables (MW DC-DC convertor and multiplier) so that the voltage could be set separately for the camera and the recorder. The camera was either fixed inside (black and white cameras) in a little additional box which served as a new lid on the top of the breeding box or if it was not possible to fix it indoor, feeding behaviour was recorded (colour cameras) from outside the nest box at a distance of around 30-40 cm. To accustom the feeding parents to the filming equipment, cameras were installed one day prior to the filming day. We recorded broods (N = 93) on the intensively-cultivated plain and additionally four broods on the slope foothills. Due to adverse weather conditions (i.e. strong rain), one brood had to be excluded from further analyses. In order to collect data about spatio-

temporal consistency of chick diet composition, parental feeding behaviour was re-filmed at 29 nestboxes that had already been filmed earlier on during former dietary assessments (Arlettaz *et al.* 2010a, Ryser *et al.* in prep). This provides a measure of diet "repeatability", i.e. a test of the assumption concerning the link between territory quality and territory occupancy.

3.3. *Analysis of film material*

From a total of 101 broods, 97 were filmed during an entire 24-h cycle, but four broods were filmed for only 7-10 h. This resulted in 2'345 h of video footage, totalling 10'557 feeding events. The videos were analyzed at 16x speed using a VLC- Player (VideoLan 1996). For each feeding event, we noted (a) which parent (male/female) was feeding, (b) the prey fed (species as far as possible, and item size) and (c) the daytime. For molecrickets and Lepidoptera larvae, prey size was divided into three distinct categories, for which we know the approximate corresponding biomass from previous studies (Arlettaz, Perrin, & Hausser 1997; Arlettaz *et al.* 2010a). Large (adult) molecrickets have an average dry biomass of 0.68 g, medium molecrickets of 0.46 g and small molecrickets of 0.36 g. For large Lepidoptera larvae we estimated an average dry biomass of 0.1 g, for medium larvae 0.08 g and for small larvae 0.06 g. To small, unidentified prey we also assigned a dry biomass of 0.06 g and to medium unknown prey a dry biomass equivalent to small molecrickets, which is 0.36 g. As predicted (Fournier & Arlettaz 2001) the four broods located on the foothill slopes had hardly any molecrickets entering the diet; they were thus excluded from the analysis linking breeding output with diet.

3.4. Spatially-explicit visualization of prey "availability"

We constructed interpolated maps for the spatial "availability" of molecricricket across the study area based on the information regarding the quantity (biomass) of molecricickets delivered to the nestlings per day for any filmed nestbox (i.e. territory) using ArcGis 10.1 (www.esri.com, Environmental Systems Research Institute, California), applying ordinary kriging. The reference area consisted of a polygon excluding both major human settlements and other unsuitable foraging and breeding areas (e.g. woodland, gravel pits, etc.). Four molecricricket categories were distinguished (see Appendices 1 & 2).

3.5. Statistical analysis

In a first step, we calculated the repeatability of our proxy for spatial molecricricket "availability" by comparing the molecricricket biomass delivered during one full day in the years 2002 (Arlettaz *et al.* 2010a), 2011 (Ryser *et al.* in prep.) and 2012 (this study) to a given nestbox, i.e. territory (see above, N = 29). Repeatability was calculated according to Lessells & Boag (1987).

Daily feeding rhythms (i.e. number of provisioning events of males and females) and molecricricket number and biomass delivered at a given nest were quantified hourly, starting at 5:00 am and ending at 21:00. These daily phenological patterns and sex specific allocation strategies were analysed using linear mixed effects models (function `'lme'`, Laird and Ware 1982).

We assessed the relationship between molecricricket "availability" (from dietary surveys in 2012) and territory occupancy rate (from 2002 through to 2012), first

with sexes grouped, and then with sexes separated. Occupancy rate was obtained from the number of years over 11 years a nest site was successfully occupied (including second broods; Arlettaz *et al.* 2010a) out of the 97 nestboxes for which video footage was collected in 2012. A nestbox could thus have been occupied theoretically up to 22 times (observed range: 1-18). This data was first analyzed by performing generalized linear mixed models (function '*glmmPQL*'; Venables and Ripley, 2002) with a binomial error distribution, and with molecricicket availability, sex and their interaction as fixed factor while nestbox, i.e. territory was a random factor.

As a proxy of reproductive output, we used both hatching and fledging success, as well as the total number of fledglings per brood. Hatching and fledgling success was analyzed by performing generalized linear mixed models (function '*glmmPQL*', Venables and Ripley, 2002) with a binomial error distribution as response variable. For both models we had nestbox (i.e. territory) as a random effect. The total number of fledglings achieved per brood was analyzed by performing a linear mixed effects model (function '*lmer*', Bates and Sarkar 2005) with gaussian error distribution, and with molecricicket availability and sex and their interaction as fixed factors and nestbox (i.e. territory) as a random effect. One nestbox had to be removed from all analyses due to too many unidentified prey items in the diet.

All statistical analyses were performed with R, version 2.13.1 (R Development Core Team, 2011) using the packages *lme4* (Bates and Maechler, 2011), *MASS* (Venables and Ripley, 2002), *lattice* (Deepayan Sarkar 2013) and *nlme* (José Pinheiro et al 2005).

4. Results

4.1. *Repeatability of dietary composition across space and time*

There was a significant repeatability of the estimated molecricricket biomass delivered to chicks between different years based on the video footage obtained from the same nestbox (2002, 2011, 2012) ($R = 0.34$, $p = 0.014$)

4.2. *Feeding pattern*

4.2.1. *Prey biomass*

In total, 101 successful (≥ 1 fledgling) broods were video-filmed in 2012, which produced 458 fledglings (mean: 4.54 chicks/brood); 32 nestboxes were used twice while 2 nestboxes were used three times, again in 2012. Molecricrickets, the primary food source, represented 38.2 % of prey item frequency and 76.7 % of delivered prey biomass. Regarding size classes, large-sized molecricrickets represented 46.1% of the whole molecricricket frequency (43.5% of biomass), while medium and small molecricrickets made up 46.0% (29.4% of biomass) and 7.9% (3.8% of biomass) of frequency, respectively. 52% of prey items were caterpillars and other insect larvae, the remaining 9.8% consisting of other prey: gryllidae, aranaeidea, earth worms, coleopterans, lizards and unknown prey (the latter making up 4% of frequency). There was no seasonal effect in the pattern of molecricricket frequency/biomass (estimate \pm SE= -0.001 ± 0.01 , $p = 0.8$, Fig S1.). For this reason we did not control for date in all subsequent analyses.

4.2.2. Daily rhythms in chick provisioning

Although males and females showed similar temporal feeding patterns during the day (time*sex: estimate \pm SE = 0.0 ± 0.03 , $F_{2, 4895} = 2.03$, $p > 0.42$), there were two distinct peaks (ca 6-9 am & 5-8 pm) with more intensive provisioning by both parents (-0.06 ± 0.02 , $F_{1, 4895} = -3.1$, $p < 0.002$, Fig. 1a). Males fed, on average, less often than females (-1.1 ± 0.42 , $F_{1, 4895} = -2.61$, $p < 0.01$, Fig. 1a), but they provisioned a greater biomass than females (0.13 ± 0.01 , $F_{1, 10009} = 855.5$, $p < 0.001$, Fig. 1b). This demonstrates that males delivered bigger prey items than females, hence essentially large molecrickets.

4.3. Fitness-related traits

4.3.1. The effects of molecricket "availability" on occupancy rate

Territory occupancy rate was affected by molecricket "availability", i.e. as available in the diet (estimate \pm SE = 0.03 ± 0.008 , $t_{1617} = 4.15$, $p < 0.001$, Fig. 2). Territories where more molecrickets were provisioned to the chicks in 2012 had a higher occupancy rate in 2002-2012. This relationship is not due merely to the number of second broods produced in a given territory: when restricting the analysis to first broods only, occupancy rate was still positively affected by molecricket "availability" (0.04 ± 0.01 , $t_{758} = 3.78$, $p < 0.001$). When sexes were considered separately, territories where males provisioned a lot of molecrickets were occupied more often over the whole study period (0.03 ± 0.009 , $t_{1595} = 4.0$, $p < 0.001$) whereas only a tendency was found in females (0.02 ± 0.01 , $t_{1595} = 1.76$, $p = 0.074$).

4.3.2. *The effect of molecrickets on current reproductive success*

The biomass of molecrickets provisioned to offspring affected the number of fledglings (estimate \pm SE = $+0.02 \pm 0.009$, $t_{198} = 2.85$, $p < 0.005$, Fig. 3a). When considering the sexes separately, there was a positive relationship between reproductive success and the biomass of molecrickets a male provisioned to the chicks (0.08 ± 0.01 , $t_{76} = 5.1$, $p < 0.001$), while no such relationship was found in females (0.01 ± 0.02 , $t_{76} = 0.7$, $p = 0.49$). The higher reproductive success of pairs feeding a greater biomass molecrickets seems to result from the combination of larger clutch sizes (0.02 ± 0.009 , $t_{184} = 2.98$, $p < 0.004$) and greater hatching (0.02 ± 0.001 , $F_{1, 275} = 6.18$, $p < 0.001$) and fledging success (0.01 ± 0.01 , $t_{278} = 4.91$, $p < 0.001$). Chick body mass was also positively associated with molecricket biomass (0.14 ± 0.05 , $t_{329} = 2.83$, $p < 0.005$, Fig. 3b), but structural size, measured via tarsus length, was not (0.01 ± 0.01 , $t_{330} = 0.65$, $p < 0.5$).

5. Discussion

This study first demonstrates considerable repeatable spatial variation in molecricket prey availability (i.e. fraction of molecricket biomass entering the diet) over an entire hoopoe population range, as obtained from video surveys carried out at the same sites over the years. This confirms our basic assumption that the relative availability of molecrickets is likely to covary in space along the time axis. Molecricket hotspots (high availability) have positive effects on current reproductive success and translate into an increased probability of territory

occupancy during the course of time. Overall, these results enable delineating areas of high value for prioritizing conservation action.

By video surveying a total of 97 out of 104 successfully occupied nestboxes in 2012, we collected dietary information from almost every brood that year on the plain of the study area. This means that we obtained an excellent coverage of the whole study area for estimating molecricricket availability throughout the reference landscape. By looking at diet in both core molecricricket areas (prey hotspots) with high hoopoe density, and marginal areas with limited occurrence of molecricrickets and low hoopoe density, we obtained enough contrast (14-100% of molecricricket biomass in diet) for building interpolated maps of the "prey landscape". This integration of marginal areas explains why the average biomass proportion of molecricrickets in the diet in the present study (77%) is lower than in a previous assessment that focused more on hoopoe core distribution areas, yielding a much higher average proportion of molecricrickets in the diet (93%; Arlettaz *et al.* 2010a). From a management viewpoint, two main hoopoe-molecricricket hotspots emerged from the analysis, which represents a spatially-explicit approach aimed at prioritizing conservation effort (see appendices). However, this interpolated map remains coarse-grained. Conservation management should further account for the different, sex-specific foraging strategies in hoopoes: if males will focus on molecricricket hotspots, females look for smaller, non-molecricricket prey items, meaning that a combination of good molecricricket hotspots and invertebrate-rich habitats could be the crux. In effect, although molecricrickets are essentially underground insects that the long bill of hoopoe males can readily extract from the soil, they can occur in very homogeneous agricultural habitats (e.g. tree plantations, Tagmann-Ioset *et al.* 2012) which may yet provide too little small-sized insects that typically crawl on

the soil surface, this latter prey category being favoured by females which have a shorter bill. The slight morphological dimorphism observed in hoopoes, in particular in beak dimensions, may thus be an adaptation to exploit slightly different trophic niches, in response to optimization of reproductive effort due to different breeding functions and tasks in the two genders. Future studies should therefore try to delineate areas across the landscape of prey where these complementary conditions are achieved, in a sort of prolongation of the fine-grained habitat selection analysis carried out by Tagmann-Ioset *et al.* (2012).

The wide range of molecricquet availabilities, through their fractions in the diet, was also prerequisite for testing the effects of the selective pressure that this locally crucial prey exerts on its major predator in Valais, the hoopoe. In the study population, molecricquets appear to dictate land-use by hoopoes, being instrumental in determining both territory quality (assessed via territory occupancy (Sergio & Newton 2003)) and reproductive performance, as evidenced through a snapshot of the breeding success in 2012. The present results largely confirm former findings that territory selection in hoopoes is a non-random process with high quality territories being settled earlier in the season and being held by dominant males (Tschumi *et al.*, in prep.). Hoopoes are thus able to perceive the spatial heterogeneity in molecricquet availability, which is probably eased by the high consistency of their spatio-temporal pattern of occurrence, as established through the repeatability analysis. Although the intrinsic quality of a territory, as mediated through molecricquet availability, seems to be essential, the observation that females lay larger clutches in molecricquet-rich areas might denote that the genetic background of adults, i.e. their intrinsic quality, plays an additional role in territory acquisition across the landscape (Village 1985; Kokko 1999, Tschumi *et al.* in prep.). Note that similar patterns emerged from a study

of lesser kestrels: molecricket consumption in the mate-feeding period was positively associated with clutch size and egg size (Catry, Franco, & Sutherland 2012). However, the observation that nestlings growing in molecricket-rich territories became heavier, while their tarsus length remained unaffected, suggests a greater role of environmental factors. In effect, tarsus length is highly heritable among birds (e.g. Smith & Dhondt 1980) while chick body mass is mainly determined by conditions experienced during growth, such as food delivery by parents. This is further supported by a higher hatching and fledging rate achieved in molecricket-rich territories, notwithstanding their higher absolute offspring productivity: again, brood mortality is likely to be determined by the amount of food provisioned, which again mostly depends on prevailing environmental circumstances. We conclude that the availability of a single prey, molecrickets, is a major component of life-time reproductive success in such a short-lived species as the hoopoe (Schaub *et al.* 2012).

The hoopoe being a multiple breeder (Arlettaz *et al.* 2010a), individual fitness depends not only on the number of fledglings produced in a single brood but also on the number of successful breeding attempts both during one season (Crick, Gibbons, & Magrath 1993) and during an individual's lifespan. Molecricket-rich territories were occupied more often than molecricket-poor territories. Given some fidelity to previous nesting site (Bötsch, Arlettaz, & Schaub 2012) and a high spatio-temporal constancy in trophic conditions (this study), adults breeding in good territories are likely to benefit from similarly higher environmental conditions in subsequent breeding events during the same or following reproductive seasons. Such additive, carry-over benefits of breeding in molecricket-rich habitats are expected to lead to significant inter-individual fitness differences that may affect population trajectory and meta-population

dynamics (Gavin & Bollinger 1988; Wiklund 1996; Forero, Donazar, & Fernando 1999; Schaub & von Hirschheydt 2009).

The fact that molecricket is an energetically extremely profitable prey (Fournier & Arlettaz 2001) and occurs abundantly on foraging grounds on the Swiss plain of the Rhone is of overriding importance given that chicks hatch asynchronously, with particularly large chicks such as hoopoe nestlings needing large prey items (Kalam & Urfi 2008). Actually, there is no other prey that is as profitable as molecrickets for hoopoes in the study area. Other large-sized insects live mostly on the soil surface and not underground: hoopoes have a long curvy beak to dig their prey out of subterranean galleries, thus facing little competition from other insectivorous predators that typically prey upon large invertebrates crawling in the stalk or on the ground.

Reproductive performance in the hoopoes breeding on the plain of the Rhone depends to a large extent on molecricket availability, which in turn seems to be conditioned by the presence of soft soils and water table levels close to the soil surface (Tschumi *et al.* in prep.). Molecrickets positively influence fitness-related traits, being a major determinant of habitat and territory quality in the study area. Habitat selection at different spatial scales – from landscape (this study) to foraging patch (Tagmann-Ioset *et al.* 2012) – appears to be crucial for the persistence of hoopoe populations. Information about the spatio-temporal dynamics of molecricket availability, hoopoe territory occupancy rate and local breeding density can thus provide the necessary guidance for efficient conservation management.

6. References

- Arlettaz, R., Fournier, J. & Zbinden, N. (2000) Evolution démographique (1979-1998) d'une population témoin de Huppe Fasciée *Upupa epops* en Valais et stratégie de conservation ciblée. *Nos Oiseaux*, **47**, 19-27.
- Arlettaz, R., Perrin, N. & Hausser, J. (1997) Trophic resource partitioning and competition between the two sibling bat species *Myotis myotis* and *Myotis blythii*. *Journal of Animal Ecology*, **66**, 897-911.
- 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 publication to public actions: When conservation biologists bridge the gap between research and implementation. *BioScience*, **60**, 835-842.
- Bächler, E., Hahn, S., Schaub, M., Arlettaz, R., Jenni, L., Fox, J.W., Afanasyev, V. & Liechti, F. (2010) Year-round tracking of small trans-Saharan migrants using light-level geolocators. *PloS ONE*, **5**, e9566.
- Bötsch, Y., Arlettaz, R. & Schaub, M. (2012) Breeding dispersal of Eurasian Hoopoes (*Upupa epops*) within and between years in relation to reproductive success, sex, and age. *The Auk*, **129**, 283-295.
- Bruinzeel, L.W., van de Pol, M. & Trierweiler, C. (2006) Competitive abilities of oystercatchers (*Haematopus ostralegus*) occupying territories of different quality. *Journal of Ornithology*, **147**, 457-463.
- Catry, I., Franco, A.M.A. & Sutherland, W.J. (2012) Landscape and weather determinants of prey availability: implications for the Lesser Kestrel *Falco naumanni*. *Ibis*, **154**, 111-123.
- Crick, H.Q.P., Gibbons, D.W. & Magrath, R.D. (1993) Seasonal changes in clutch size in British birds. *Journal of Animal Ecology*, **62**, 263-273.
- Ens, B.J., Kersten, M., Brenninkmeijer, A. & Huschler, J.B. (1995) Territory quality, parental effort and reproductive success of oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology*, **61**, 703-715.
- Forero, M.G., Donazar, J.B. & Fernando, H. (1999) Causes and consequences of territory change and breeding dispersal distance in the black kite. *Ecology*, **80**, 1298-1310.
- 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.

- Fretwell, S.D. & Lucas, H.L. (1969) On territorial behavior and other factors influencing distribution in birds. *Acta Biotheoretica*, **19**, 16–36.
- Gavin, T.A. & Bollinger, E.K. (1988) Reproductive correlates of breeding-site fidelity in Bobolinks (*Dolichonyx Oryzivorus*). *Ecology*, **69**, 96–103.
- Hegner, R.E. & Wingfield, J.C. (1987) Effects of brood-size manipulations on parental investment, breeding success, and reproductive endocrinology of House Sparrows. *The Auk*, **104**, 470–480.
- Kalam, A. & Urfi, A.J. (2008) Foraging behaviour and prey size of the painted stork. *Journal of Zoology*, **274**, 198–204.
- Kokko, H. (1999) Competition for early arrival in migratory birds. *Journal of Animal Ecology*, **68**, 940–950.
- Korpimäki, E. (1988) Costs of reproduction and success of manipulated broods under varying food conditions in Tengmalm's owl. *Journal of Animal Ecology*, **57**, 1027–1039.
- Lambrechts, M.M., Caro, S., Charmantier, A., Gross, N., Galan, M.-J., Perret, P., Cartan-Son, M., Dias, P.C., Blondel, J. & Thomas, D.W. (2004) Habitat quality as a predictor of spatial variation in blue tit reproductive performance: a multi-plot analysis in a heterogeneous landscape. *Oecologia*, **141**, 555–561.
- Lessells, C.M. & Boag, P.T. (1987) Unrepeatable repeatabilities: a common mistake. *The Auk*, **104**, 116–121.
- Martin, T.E. (1987) Food as a limit on breeding birds: A life-history perspective. *Annual Review of Ecology and Systematics*, **18**, 453–487.
- Martín-vivaldi, M., Palomino, J.J., Soler, M. & Soler, J.J. (1999) Determinants of reproductive success in the hoopoe. *Bird Study*, **46**, 205–216.
- Van Noordwijk, A.J., McCleery, R.H. & Perrins, C.M. (1995) Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. *Journal of Animal Ecology*, **64**, 451–458.
- Orians, G.H. & Wittenberger, J.F. (1991) Spatial and temporal scales in habitat selection. *The American Naturalist*, **137**, 29–49.
- Perrins, C. (1964) Survival of young swifts in relation to brood-size. *Nature*, **201**, 1147–1148.
- Perrins, C. (1965) Population fluctuations and clutch-size in the great tit, *Parus major* L. *Journal of Animal Ecology*, **34**, 601–647.
- Richner, H. (1992) The effect of extra food on fitness in breeding carrion crows. *Ecology*, **73**, 330–335.

- Schaub, M. & von Hirschheydt, J. (2009) Effect of current reproduction on apparent survival, breeding dispersal, and future reproduction in barn swallows assessed by multistate capture-recapture models. *The Journal of animal ecology*, **78**, 625–35.
- 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.
- Schaub, M., Reichlin, T.S., Abadi, F., Kéry, M., Jenni, L. & Arlettaz, R. (2012) The demographic drivers of local population dynamics in two rare migratory birds. *Oecologia*, **168**, 97–108.
- Sergio, F. & Newton, I. (2003) Occupancy as a measure of territory quality. *Journal of Animal Ecology*, **72**, 857–865.
- Simons, L.S. & Martin, T.E. (1990) Food limitation of avian reproduction: An experiment with the Cactus Wren. *Ecology*, **71**, 869–876.
- Smith, J.N.M. & Dhondt, A.A. (1980) Experimental Confirmation of Heritable Morphological Variation in a Natural Population of Song Sparrows. *Evolution*, **34**, 1155–1158.
- 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.
- Tremblay, I., Thomas, D.W., Lambrechts, M.M., Blondel, J. & Perret, P. (2003) Variation in Blue Tit breeding performance across gradients in habitat richness. *Ecology*, **84**, 3033–3043.
- Valcu, M. & Kempenaers, B. (2008) Causes and consequences of breeding dispersal and divorce in a blue tit, *Cyanistes caeruleus*, population. *Animal Behaviour*, **75**, 1949–1963.
- Valkama, J., Korpimäki, E., Holm, A. & Hakkarainen, H. (2002) Hatching asynchrony and brood reduction in Tengmalm's owl *Aegolius funereus*: the role of temporal and spatial variation in food abundance. *Oecologia*, **133**, 334–341.
- Village, A. (1985) Spring arrival times and assortative mating of kestrels in south Scotland. *Journal of Animal Ecology*, **54**, 857–868.
- Wiklund, C.G. (1996) Determinants of dispersal in breeding merlins (*Falco Columbarius*). *Ecology*, **77**, 1920–1927.
- Williams, J.B., Plessis, M.A. & Siegfried, W.R. (1991) Green Woodhoopoes (*Phoeniculus purpureus*) and Obligate Cavity Roosting Provide a Test of the Thermoregulatory Insufficiency Hypothesis. *Auk*, **108**, 285–293.

7. Acknowledgements

We would like to thank Yves Bötsch for providing basic information about the study species, Murielle Perron, Jaël Hoffmann and Rien van Wijk who helped in the field and did most of the nestbox controls, as well as bird captures and ringing. We are also grateful to Olivier Roth for access to the library. Finally, we want to thank Maria Berchtold and Louis Sutter for their assistance and mental support.

8. Figure legends

Figure 1: Mean (\pm SE) (a) number of provisioning events and (b) provisioned biomass (dry g) by females and males with respect to daytime (h). Although females delivered food items more often, males delivered more biomass, i.e. fed on average much larger prey items.

Figure 2: Relationship (curved, estimated from logistic regression) between territory occupancy rate and the biomass of molecrickets entering the diet in different nest sites, i.e. territories. The grey bars indicate the frequency distribution of molecrickets in diet (lower X axis) of the observed event.

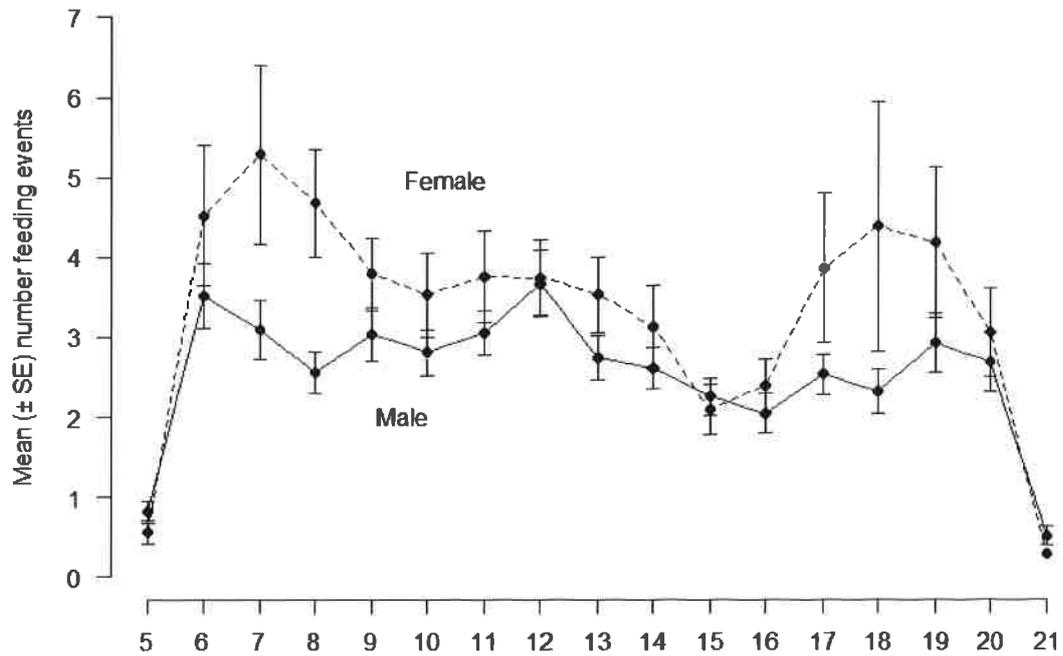
Figure 3a: Relationship between (a) the number of fledglings and (b) mean chick body mass (in g) (\pm SE) vs. the molecricet biomass entering the diet at a given nestbox. The lines are regression lines. Body mass was measured at ca. day 18 of age, i.e. a few days before fledging.

Figure S1: Mean molecricet biomass (estimated dry mass) delivered to the nestlings (at age 11-15 days) by parents over the whole breeding season.

9. Figures

Figure 1

a)



b)

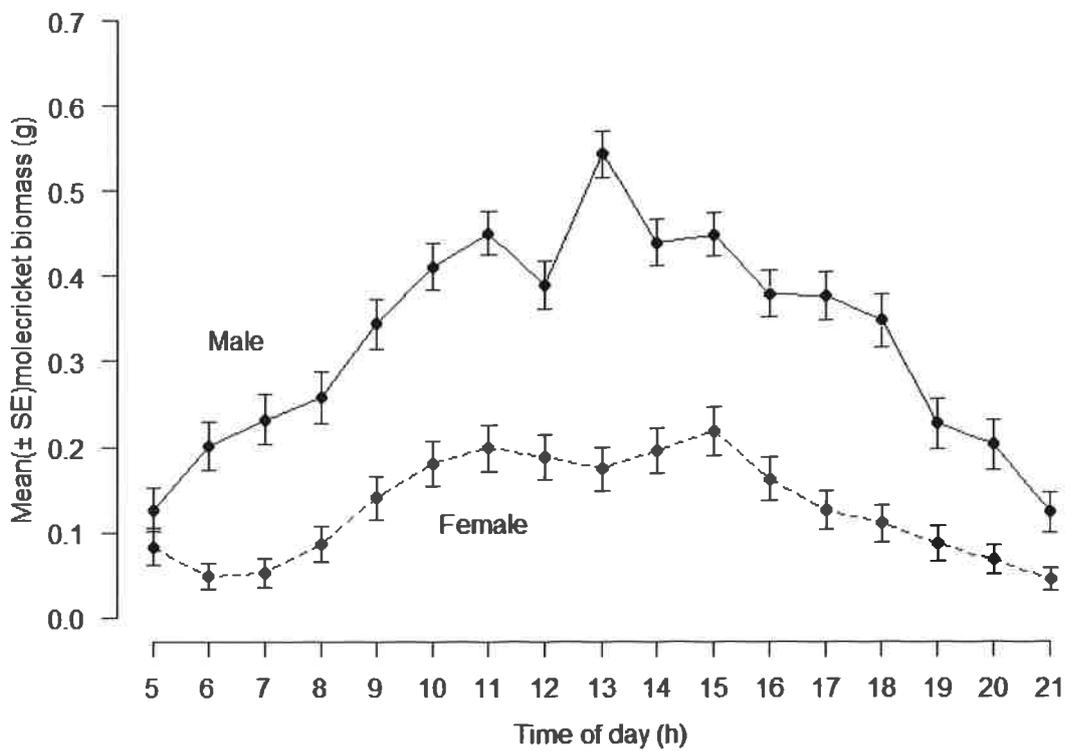


Figure 2

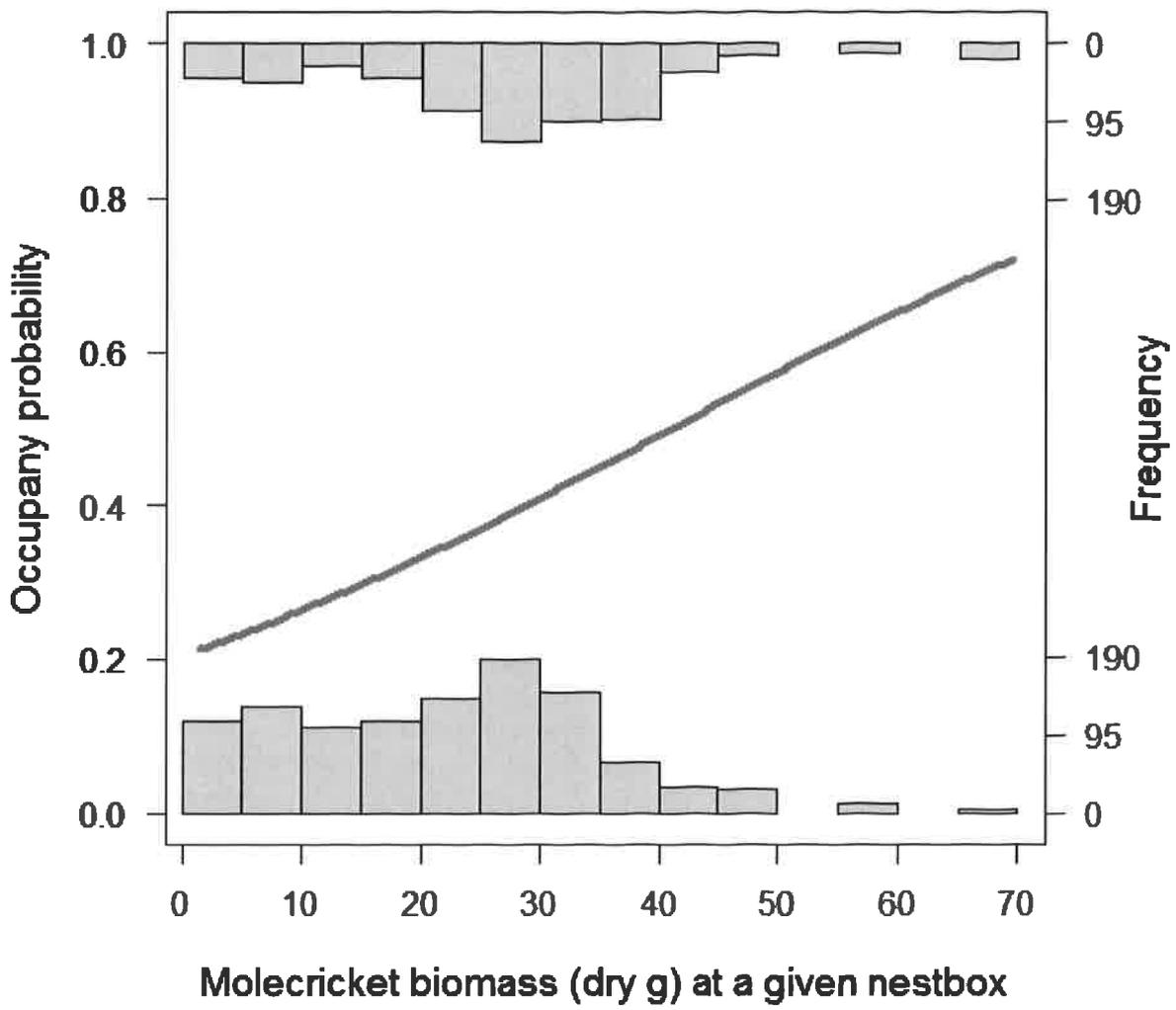
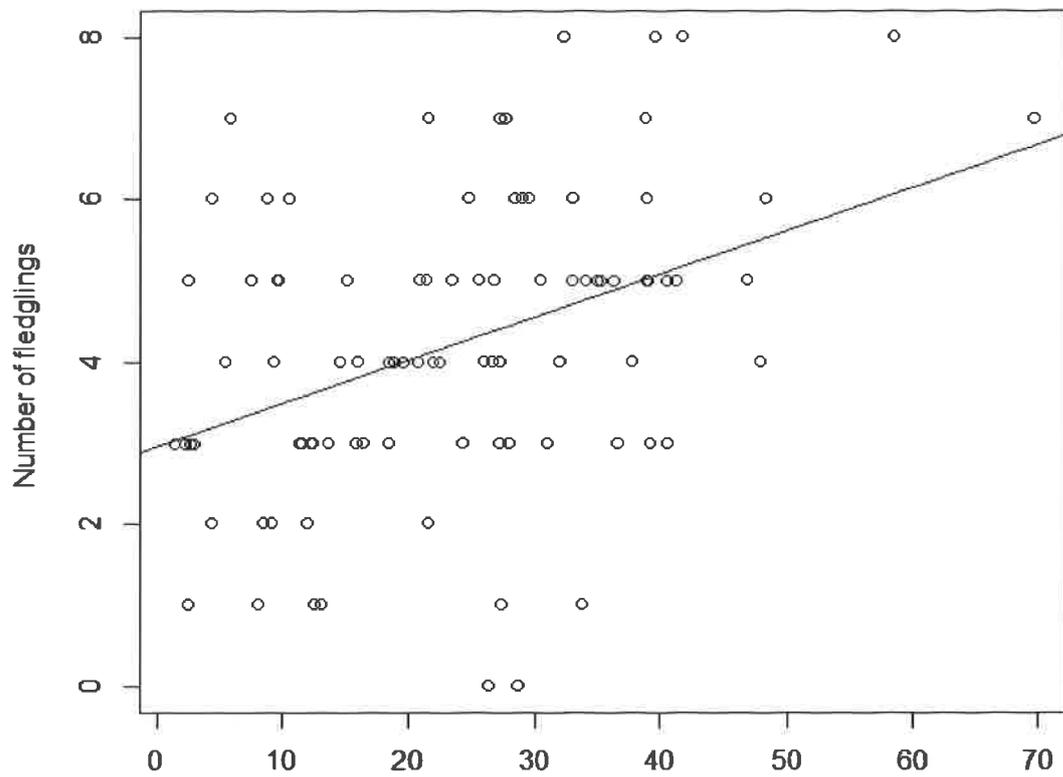
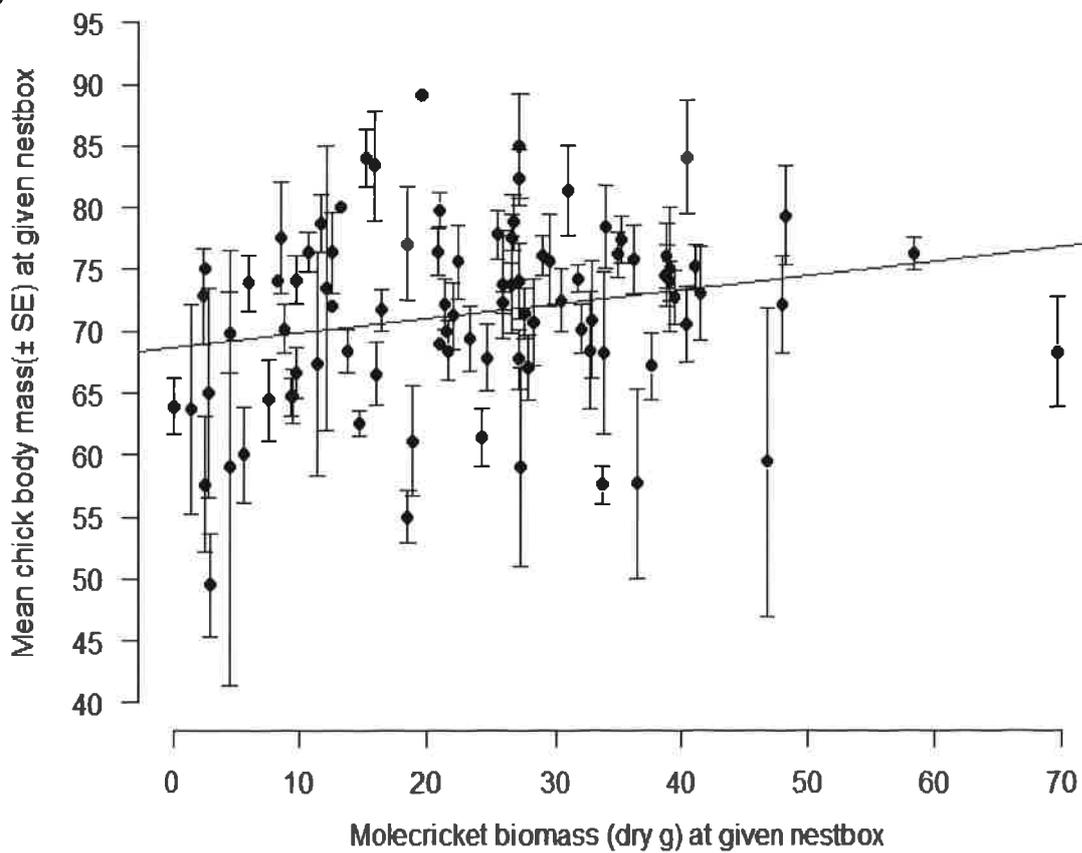


Figure 3

a)



b)



10. Appendix



Appendix 1: Interpolated map of molecricket estimated “availability” between Fully-Charrat and Riddes, one of the two delineated molecricket hotspots. Darker the colour higher the availability as measured in terms of biomass provisioned to nestlings during one day (1-17 g: yellow; 18-34 g: orange; 35-52 g: red; 53-69 g: dark red).



Appendix 2: Idem as Appendix 1, but for the area located between Bramois and Grône.