Determinants of reproductive success in an endangered, recovering hoopoe population

Diplomarbeit

der Philosophisch-naturwissenschaftlichen Fakultät
der Universität Bern

vorgelegt von

Patricia Portner

2008

Leiter der Arbeit:
Dr. M. Schaub & Prof. Dr. R. Arlettaz
Conservation Biology
Zoologisches Institut, Universität Bern

Table of contents

Abstract *2*

Introduction *3*

Material and Methods *5*

Field work **5**

Study site 5

Reproductive and morphological data 5

Mole cricket occurrence 7

Statistical analyses **8**

Morphological data 8

Mole cricket occurrence 9

Modelling reproductive output 11

Results *12*

Reproductive output 12

Morphological data 13

Mole cricket occurrence 13

Modelling reproductive output 14

Discussion *15*

Acknowledgements *19*

References *20*

Tables *24*

Figure captions *33*

Figures *34*

Appendix *36*

Abstract

The identification of crucial resources is of paramount importance for the efficient conservation of endangered species. Also essential is the understanding of the links between patterns of resource exploitation, reproductive success and individual attributes. We investigated the relationships between reproductive performance, individual characteristics (various morphological traits) and habitat quality (availability of mole crickets, a favourite prey locally) in an endangered recovering population of the hoopoe (*Upupa epops*) in the Swiss Alps. Reproductive success was influenced positively by mole cricket occurrence, negatively by hatching date, and correlated in different manners with certain morphological characteristics of the adults; the age of the male parent, and bill and crest lengths of the female correlated positively with fledgling number. Detectability of mole cricket galleries was influenced negatively by ground vegetation density and positively by the amount of bare ground. The occurrence of mole crickets depended primarily on the availability of sandy, non-gravelly soils, showing that appropriate habitat selection is an essential component of reproductive performance in the hoopoe. As mole crickets appear to constitute a staple diet for breeding hoopoes beyond our study population, we recommend that hoopoe conservation plans developed in Central Europe account for mole cricket availability.

Key-words: reproductive success, morphological characteristics, habitat quality, species conservation

Introduction

Survival and reproduction depend on resources which are hardly ever available *ad libitum*, whilst individuals differ in their attributes. This elicits competition for access to resources, i.e. a non-equal share of resources among individuals (Bruinzeel, van de Pol & Trierweiler 2006). In order to maximize fitness, individuals attempt to acquire a sufficient amount of crucial resources, and their ability to do so is often correlated with traits reflecting individual's quality (Bruinzeel, van de Pol & Trierweiler 2006). In birds, such traits are body size (Verhulst, Perrins & Riddington 1997; Barbraud *et al.* 1999), plumage coloration (Fugle *et al.* 1984) and song characteristics (Gil & Gahr 2002; Martín-Vivaldi, Palomino & Soler 1998). When only high quality individuals can afford to invest in the development of such traits, these traits are assumed to function as honest signals of individual quality (Griggio *et al.* 2007). In intersexual and intrasexual communication, honest signals play a major role, e.g. in the selection of mates or in agonistic signalling (Loyau, Saint Jalme & Sorci 2005). Honest signals involved in agonistic signalling provide the potential to settle competitive contests and thus establish social hierarchy without physical interactions like fights. Independent of the processes involved in creating social hierarchy, the social status of an individual has consequences on its ability to access essential resources such as food, mates and breeding sites. Dominant individuals have a priority access to resources over subordinates, resulting in unequal resource allocation between individuals differing in hierarchical status (van Oort *et al.* 2007). Habitat quality can vary drastically among sites in terms of availability of critical resources and is thus an important determinant of individual fitness, especially for territorial animals. Migratory birds have to select a new territory each year. Birds which arrive early on the breeding grounds usually occupy the best territories first, out-competing late-arriving birds (Forstmeier 2002; Mermod 2008). As high quality individuals tend to arrive earlier

at the breeding sites, one would expect territory quality to correlate positively with individual quality (Bruinzeel, van de Pol & Trierweiler 2006).

Given the assumption that high quality individuals should acquire greater amounts of a resource, fitness components of such individuals should be enhanced compared with lower quality individuals. Typical fitness components are size at birth, growth pattern, age/size at maturity, number, size and sex ratio of offspring, age-/size-specific reproductive investments, age- and size-specific mortality schedules or life span (Stearns 1976). Relatively easy to assess in the field, reproductive output in terms of clutch size and number of fledglings thus allows inferences about an individual's quality and the quality of the territory it is occupying.

Previous investigations in our research group have suggested that territory quality in an endangered, recovering population of the hoopoe in the upper Rhône valley (Valais, SW Switzerland) may be in first line determined by the local abundance and accessibility of mole crickets (Fournier & Arlettaz 2001; Ioset 2007). This large orthopteran, which lives in underground galleries, is the favourite prey of hoopoes in Valais, where it makes up to 93% of the total biomass provisioned to chicks (Fournier & Arlettaz 2001; Schaad 2002). As nesting sites can no longer be considered as a limiting factor after the installation of hundreds of nest boxes in the focal hoopoe population (Arlettaz *et al.*, in prep.), we predicted first that reproductive output (here measured as clutch size and number of fledglings) should nowadays be influenced mostly by mole cricket availability. Secondly, we hypothesized that individuals capable of occupying habitats where mole crickets abound should be of higher quality than individuals breeding in habitats in which prey is scarce. We thus expected individual quality to be manifested in morphological characteristics (body linear dimensions, plumage patterns and measure of somatic symmetry) that are potentially involved in mate choice and reproductive strategies; these traits were measured in

the field from captured birds. Trough the identification of the subtle links between food resource availability, reproductive performance and individual attributes we hoped, ultimately, to find ways of assessing habitat suitability for the hoopoe population in order to optimize conservation management. Finding morphological surrogates of individual quality, which could assist field workers in their assessments of local population status, is another conservation goal of this study.

Material and Methods

Field work

Study site

The study was carried out in the Upper Rhône valley (Valais, southwestern Swiss Alps; 46°07'N, 07°08'N) between Vernayaz and Sierre, from April to July 2007. The whole study area has an extension of ca. 64 km^2. Since the 1950s and 1960s, the study area has been intensively used for agricultural purposes (predominantly dwarf fruit tree plantations and vineyards; Fournier & Arlettaz 2001). For a detailed description of landscape, climate and vegetation of this area see Arlettaz (1984) and Fournier (1991). As the availability of natural cavities was defined as a serious limiting factor for that population (Fournier & Arlettaz 2001), more than 700 nest boxes were installed in agricultural sheds and buildings since 1999 (Arlettaz *et al*., in prep.). This led to a dramatic increase of the population in the following years (Arlettaz *et al.*, in prep.).

Reproductive and morphological data

Every second week, nest boxes were inspected visually through the entrance hole using a mirror and a torch. Occupied boxes were subsequently visited approximately every 3rd day and the number of eggs and hatchlings recorded at each visit. If the entire clutch was visible, this was recorded as an «exact clutch size»; only exact clutch

sizes were analysed subsequently. We captured the adults after chicks had hatched using mist-nets (3 m length, 35 mm mesh size) or traps that were placed directly in front of the entrance hole of the nest box. Whenever possible, advanced brooding females were captured delicately by hand from opening the nest box.

We caught 74 adult males and 85 adult females. All birds were ringed, sexed (the uropygial gland is much more devoped in females; Schaad 2002) and weighed (accuracy 0.5 g); the lengths of primary feather 5 (P5) and 1st tail feather were measured using a ruler (accuracy 0.5 mm). Additionally, the lengths of tarsus («bent toes» method; Svensson 1992), crest (from the proximal end of the nostril to the end of the longest crest feather) and bill (from the bill tip to the distal end of the nostril) were measured using dial callipers (accuracy 0.1 mm). Measurements of P5 were taken from the left and right wings. All traits were measured twice except weight. Furthermore, digital pictures of the spread tail were taken to analyse the relationship between a distinctive plumage pattern that is thought to play a role in mating choice: during field observation, it has been noticed that receptive females frequently present their back to territorial calling males, while widely spreading out their tail feathers (R. Arlettaz, unpublished). The contrasted black-white stripe in the middle part of the tail shows interindividual variation, with some hoopoes having a very regular stripe whereas others exhibit a very chaotic stripe design (Fig. 1). To quantify the irregularity of the tail stripe (Fig. 1), a polygon on digital pictures of the spread tails was drawn with program Image J (http://rsb.info.nih.gov/ij). This polygon represented an «idealized tail stripe», defined by the outer limits of the white areas on the rachis (Fig. 1). The area of white parts of the original tail stripe which exceeded the limits of the «idealized stripe» was measured as well as the black areas within the «idealized stripe». The ratio of the sum of all white and black areas to the area of the «idealized tail stripe» was calculated. This

allowed correcting for the size of the tail and for the extent of spreading out.

In total 552 nestlings (when older than 17 days old and with at least 50 g body mass) were ringed and weighed. The number of fledglings was estimated from regular controls close and after breeding completion.

Mole cricket occurrence

In order to assess mole cricket distribution across the study area we selected 120 plots (at least 100 m apart) using a partially stratified sampling design (Arcview v3.3 software; Environmental Systems Research Institute Inc., California). Based on previous knowledge of habitat preferences (Ioset 2007), we focused on orchards and tree fruit plantations. Given that we hypothesized (based on Fournier & Arlettaz 2001) that mole crickets prefer soft and wet soils, and so as to increase contrast in our dataset, we fist selected 10 plots each at places with a high and a low water table (0.5 – 1.5 m below the soil surface and deeper than 4.5 m, respectively). Second, 10 plots were situated in regions with gravelly soil, because this soil type is relatively rare in the study area, and again to obtain sufficient contrast. The locations of the remaining 90 plots were randomly selected irrespective of soil type and ground water table level. We prospected for mole crickets by walking three 10 m deep transects into orchards, between tree rows, starting from orchard edge, i.e. from the closest road or track. The three transects were themselves separated by three tree rows in between. Focal tree rows were marked with poles for subsequent visits. Because mole crickets are ground-dwelling orthopterans which rarely emerge to the soil surface (Jacobs & Renner 1974), we had to look for entrance holes to their underground galleries. The three transects were searched for a total of 10 min and presence/absence of galleries was recorded. Because the detection probability of mole crickets galleries probably depends on grass density and proportion of bare ground, these co-

variables we also recorded at each visit. Each plot was visited five times during the season, every 11th day starting in late May.

Statistical analyses

Morphological data

We first tested whether hoopoes are sexually size dimorphic. A two-sample t-test (Nudds & Kaminski 1984) showed that both the mean (± SD) length of primary P5 (♂: 119.14 ± 3.50 mm, n = 73; ♀: 114.06 ± 3.54 mm, n = 82; t = 8.97, p< 0.05) as well as the mean tarsus length (♂: 23.76 ± 0.89 mm, n = 73; ♀: 22.90 ± 0.86 mm, n = 84; t = 6.21, p < 0.05) differed between sexes. Therefore, the two sexes were treated separately in subsequent analyses. A PCA was then performed using body mass as well as the mean lengths of, respectively: tarsus (average of left and right tarsus lengths), P5 (same), 1st tail feather, crest and bill. This was intended to reduce the number of morphological variables for the final model. As the variables had different units a correlation matrix approach was applied.

Repeatability tests were carried out for the measurement of the tail stripe (Lessells & Boag 1987). First, ten tails were measured twice on photographs, showing high repeatability (F = 127.38, r = 0.88; df = 4,5; p < 0.01). Second, five individuals from which several pictures were available spanning the entire breeding season again showed a high measurement repeatability (F = 3820.52, r = 0.99; df = 9,10; p < 0.01). This indicates that the method is suitable even with variations in the extension of spreading.

To investigate whether patterns of fluctuating asymmetry were present, differences between left and right P5 primaries were analysed. Fluctuating asymmetries are minor environmentally induced departures from perfect symmetry of a bilateral trait and thus reflect developmental noise (Palmer & Strobeck 1986). First, we checked whether the measurements were repeatable (F = 45.44, r = 0.85; df =6,21; p< 0.01) and thus immune from measurement errors. Because the exhibition of fluctuating asymmetry is not driven towards either

body side, the deviations are expected to be normally distributed around zero. The observed differences between left and right P5 primaries were normally distributed (Shapiro-Wilk normality test: W = 0.98, p = 0.34, n = 84), with a mean not deviating from zero (two-sample Kolmogorov-Smirnov-test: D = 0.179; p-value = 0.14, n = 84). Thus, the deviations between left and right P5 primaries fulfilled the underlying assumptions. The unsigned deviations between right and left body side were included in the final model.

We used Program R (R Development Core Team 2004) to conduct these statistical tests.

Mole cricket occurrence

Mole cricket gallery presence/absence data were analysed by applying occupancy models (MacKenzie *et al.* 2002) implemented in MARK (White & Burnham 1999). These models allow separating the probability that a plot is occupied from the probability that occupancy of an occupied plot is detected. Each process (occupancy, detection) can be modelled as a function of different variables. Presence or absence of mole cricket galleries was recorded for each of the 3 tree rows in each plot. As presence and absence were highly consistent between the three transects within a plot, the information was combined to only one value per plot and visit.

Soil type and water table height at plot location were included as factors potentially influencing the occurrence (occupancy probability) of mole crickets. The information about local water table height was extracted from a map provided by the Service des Routes et Cours d'Eau, Canton du Valais (Appendix 2). Point measurements of soil samples (data provided by the same governmental agency; Appendix 3) were used to assess which soil type most likely prevailed at a study plot by assigning the soil type of the closest point with measurement (maximal distance 1 km). As the horizontal parts of mole cricket galleries are located in the first 20 cm below soil surface (Jacobs &

Renner 1974), only the soil measurements of the first horizon were considered. To simplify the highly diverse matrix about soil type, five categories were defined which grouped similar soil types with respect to the hypothesised preferences of mole crickets for certain soil textures (Appendix 4). The first two categories contained predominantly silty soils within a mostly fine-grained matrix: category one with no-till-limited presence of sand and category 2 with obvious presence of sand. The third and fourth categories consisted of predominantly sandy soil: category three with sand embedded in a matrix dominated by gravel, stones or pebbles, whereas the fourth category contained sandy soils where large structures such as gravel and pebbles were absent. Finally, the fifth group contained all kinds of vegetal soil (decomposed litter) irrespective of their amount of silt or sand. Mole cricket occurrence was expected to be considerably higher in the fourth category (Fournier & Arlettaz 2001), therefore occupancy was modelled with respect to this specific prediction. Moreover, we expected detection of mole cricket galleries to be influenced by the amount of bare ground and vegetation density (grass height), and therefore considered these co-variables to model detection probability. We finally formulated occupancy models considering different combinations of variables potentially affecting mole cricket gallery occurrence and detection. We ranked the model according to their fit to the data using Akaike's Information Criterion (AIC) and AIC weights (Burnham & Anderson 1998).

Based on the results from the occupancy model, habitat quality for hoopoes was estimated via the spatial distribution of mole cricket occurrence, under the assumption that the occurrence of this prey is the main determinant of habitat quality (Fournier & Arlettaz 2001). Mole cricket availability *per se* (which accounts for both abundance and accessibility) could not be assessed here for obvious practical reasons (Ioset 2007). Because mole cricket occurrence was affected by soil type (see results), we looked at the typology of soils occurring within a 479 m radius around occupied nest boxes; this radius corresponds to a

circular home range size of 72.2 ha, which is the largest home range size observed locally (radiotracking data, Ioset 2007). Since one single soil category showed a distinctively higher mole cricket occupancy, the proportion of soil samples belonging to this category relative to all available soil samples within these 479 m radii was multiplied by the corresponding mole cricket occupancy estimate. The same was done for the remaining soil type samples belonging to the other soil type categories. The sum of these values within a given homerange was included in the final model as a mole cricket index (MCI) representing habitat quality at a given nest site.

Modelling reproductive output

To investigate how reproductive output was associated with individual quality and with the occurrence of mole crickets, general linear mixed models were used (GLMM; package R glmmML library), assuming poisson distributed residuals and a log link function (hereafter termed final models). The models with clutch size as a response variable (performed for males and females separately) included following explanatory variables: hatching date, age of the breeding individual (controls of nestlings ringed in previous years), breeding trial within the season (one male was involved in three successive broods, see Results), PCA scores for morphological attributes and mole cricket index (MCI). For the analysis of the number of fledglings, the same structure and explanatory variables were used, but weather parameters were added because there are known to affect productivity (Arlettaz *et al.*, in prep.). For this purpose, we used information about ambient temperature and rainfall during the 30 days following hatching. The latter two variables were not included alternatively in the various possible model combinations, but present in every model as general background factors. This is because we did not make specific inferences regarding them. Individual was used as a random effect in every model as some individuals were captured at different nest sites.

The best models were defined with an abbreviated model selection procedure and according to the dAIC: fist, all possible combinations of variables within the first group including hatching date and breeding attempt were performed, with all other variables systematically included. Models with dAIC ≤ 1.5 were identified as supported by the data and only the variables included in these models were used for the next modelling step. The second modelling step was to keep fixed the variables or variable combinations of the first group included in the best models, with this time the variables of group 2 (PCA scores) varied in all possible combinations. Third, the best models (dAIC ≤ 1.5) were selected, with this time the variables of the 3rd group (bird age and MIC) being combined in all possible manners. By this procedure (abbreviated model selection), the vast numbers of possible variable combinations was reduced by grouping the variables and proceeding only with variables included in the best models within a group. During the fourth, last step, model averaging (Burnham & Anderson 2002) for the resulting best models (dAIC ≤ 1.5) was performed.

Because there was only very limited data about irregularity of the tail stripe and fluctuating asymmetry, it was not possible to include these variables in sex-specific models. Therefore, we performed another complete series of analyses as described above, with all variables considered, but without discriminating between the sexes. Because for the same brood, both male and female may have provided information about the tail pattern, we used the brood number as an additional random effect. Otherwise, model selection followed the same principles as above.

Results

Reproductive output

From a total of 164 broods, 119 were successful, i.e. produced at least one fledgling. Thirty-seven females and 13 males were recaptured while

involved in a second brood, with one male even involved in a third brood. The mean (±SD) clutch size was 7.23 (±1.3; n = 115) and the mean number of fledglings was 4.44 (±1.91; n = 119).

Morphological data

The first three principal components of the PCA (PC1-3) explained 73.4% and 70% of the variance for the females and males, respectively; they were therefore retained in the final model (Table 1). PC1 correlated positively (high positive loadings, Table 1) with measurements of linear body traits. Individuals with relatively short feathers, large tarsi and high body mass had high scores for PC2. PC3 for both females and males revealed a negative correlation between tarsus length vs. crest and bill lengths. In addition, a very strong negative correlation between body mass and crest and bill lengths was observed in females. The irregularity of tail stripe ranged from 7.41% to 48.47% (n = 32) for females and from 4.28% to 43.90% (n = 29) for males, where 0% would correspond to a total regular tail stripe.

Mole cricket occurrence

Nine out of 120 plots had to be excluded from the occupancy analysis because there was either no soil type measurement within 1 km or no water table level information available.

Modelling detection and occurrence of mole cricket galleries revealed (first best model) that detection was affected negatively by grass height (i.e. grass vegetation density) and positively by the amount of bare ground, whereas mole cricket occurrence depended on soil type, with a preference for sandy, non-gravelly soil (category 4; Table 2). In contrast, there was some uncertainty regarding the impact of the water table level on mole cricket occurrence as this factor did not appear in the first ranked model. The second best model actually included that factor, but it had about 2.4 times less support than the best model. Concerning the preference of mole crickets for sandy, non-

gravelly soil, the probability of plot occupancy was 0.471±0.121 for sandy soil, but dropped to 0.194±0.041 for all other soil types.

Of 138 occupied nest boxes, 106 had at least one soil sample within the «theoretical» circular homerange delineated around the nest site (mean = 7.2, maximum = 26; see Methods), which allowed the calculation of a mole cricket index (MCI). Fourty-five homeranges did not have sandy, non-gravelly soil; they were therefore attributed a low MCI value of 0.194 (0 x 0.471 + 1 x 0.194). In contrast, homeranges which consisted entirely or almost entirely of sandy, non-gravelly soil obtained a MCI of 0.471 (n=9). The distribution of the MCI is shown in Fig. 2. Most homeranges had a low MCI and few reached the maximum possible value.

Modelling reproductive output

Clutch size was negatively associated with hatching date in both females (Table 3) and males (Table 4). The later in the season an individual started to breed, the smaller was its clutch (Table 9). Morphological traits, mole cricket index and the age of the breeding individual had no impact on clutch size in both sexes (Tables 3 and 4).

The number of fledglings was also negatively associated with hatching date for both females and males (Tables 5 and 6), and with the number of breeding attempts by a female during the entire season of reproduction. The number of fledglings was positively affected by scores from the female's PC3 which in turn had positive loadings of crest and bill length and a negative loading of weight (Table 1). Reproductive output in terms of the number of fledglings decreased with the age of the male parent (Table 6). Furthermore, the mole cricket index (MCI) was positively associated with the number of fledglings for males (Figure 3).

Clutch size analysed with the combined data (males and females; Table 8) was not affected by any considered explanatory variable. The number of fledglings analysed with the combined data was affected by hatching date and age of the breeding individual. In the second best

model there was also an effect of the irregularity of tail stripe (Table 9). Individuals breeding later in the season thus had a lower reproductive output than individuals reproducing earlier. The reproductive output was positively associated with the irregularity of the tail stripe, meaning that more irregular individuals had more offspring than individuals with regular tail stripes.

Discussion

Our analyses confirmed the assumption that mole crickets prefer soft soils. Sampled plots with sandy, non-gravelly soil had a 2.4 times higher probability to be occupied by mole crickets than sampled plots with other soil types. The finding of this distinction between sandy, non-gravelly soil and other soil types represents a more precise specification of the hypothesis that mole crickets prefer soft soil, as vegetal soil, which can also be regarded as soft soil, had a occupancy probability not differing from the occupancy probability of hard soil types. Thus, the crucial characteristic of a soil concerning mole cricket occurrence might rather be the amount of sand than the softness per se, even though a high amount of sand also implicates softness. Although not being included in the best model, a trend for a positive correlation between ground water table height and mole cricket occupancy was represented in the second best model, indicating that wet soils are probably preferred by mole crickets.

Like it is found in many bird species, clutch size was consistently negatively affected by hatching date (Klomp 1970; Meijer, Daan & Hall 1990; Verhulst, van Balen & Tinbergen 1995). Broods decreased in size with increasing time within the season. This can be viewed in the context of migration. Before leaving to the wintering sites, individuals have to spend some time on food uptake for fat storage which is shortened when the time spent on breeding and food provisioning to fledglings is prolongated. Especially for hoopoes, showing asynchronous hatching (Martín-Vivaldi *et al.* 1999), a large brood late in season would

extend the time period of parental care. Given the effect of hatching date, one would expect the number of breeding attempt to have an accordingly negative effect on clutch size. Nevertheless, this variable was included in neither of the best sex-specific models. However, this might be artefactual as not the entire breeding population was captured and therefore some broods might have been falsely assigned to first broods when breeding individuals were captured for the first time in the season. In fact, individuals might have either bred earlier in natural cavities or they might have simply not been caught during earlier breeding. The former explanation is rather unlikely, as the installation of nest boxes took place because natural cavities are very scarce, whereas artificial breeding cavities are nowadays highly abundant.

Morphology of the parents was not important for the variation of clutch size. This can be interpreted in the context of conditional brood reduction strategy in hoopoes and accompanying optimistic clutch sizes (Martín-Vivaldi *et al.* 1999). Hence, inter-individual differences should become manifested mainly in the number of offspring surviving, being an important determinant of parental fitness. The sex-combined best model did not include any of the explanatory variables, potentially due to the very low sample size.

The third principal component was included for females in the best models explaining the number of fledglings. As the first principal component did roughly account for overall size differences, the third component accounted more for subtle differences, with females showing larger traits concerning the head region (bill and tarsus length) and a lower weight, when having higher principal component scores. As the model averaged estimator for the third PC was positive, females with larger crest and bill and a lower weight showed to have more fledglings compared to females not showing such characteristics. Even though it could be expected that heavier females should be able to invest (in absolute terms) more of their body reserves in reproduction without decreasing their own weight to a huge extent, the results did not

support this hypothesis. As lighter females had more fledglings, one could also argue that females of high individual quality can afford to invest much of their body fat reserves without lowering their own survival, because they show fast body fat restorage ability during the period between the end of reproduction and the onset of fall migration and between the reproductive attempts themselves. That the same trend (lighter females having more fledglings) was not detected for males could be due to the different manners of parental investment for males and females. The irregularity of tail stripe was included in the best sex-combined model explaining fledgling number. The finding that the association between irregularity of tail stripe and number of fledglings was positive is somehow difficult to interpret, as the association was expected to be negative. Thus it can not be distinguished between a failure of the applied method and erroneous expectations about the function of tail stripe in honest signalling. Furthermore, the sample size in the sex-combined model was very low. It can be hypothesised that an increase of the sample size and a distinction of sexes could reveal different patterns concerning the influence of the tail stripe on reproduction.

Furthermore, clutch size decreased with increasing age of the male. This was true for sex-separated models as well as for sex-combined models. It was shown before that in general, older individuals have a reduced fertility due to senescence and thus producing less offspring (Fisher 1930).

The reproductive output is in general closely linked with the availability of food resources (Martin 1987). The mole cricket index (MCI) was positively associated with the number of fledglings; this was only true for the male sex-specific model. This fortified the finding of other studies which highlighted the special importance of mole crickets as a diet component of nestlings (Fournier & Arlettaz 2001; Schaad 2002). Males breeding in regions with a high mole cricket index thus had a fitness benefit compared to males breeding at sites where sandy, non-

gravelly soil is scarce and hence the mole cricket abundance is low. Therefore, competition for nest boxes situated in regions with sandy, non-gravelly soil is expected to occur.
This study combined potential parameters of individual quality with habitat quality aiming at explaining reproductive parameters such as clutch size and number of fledglings. Even though it is difficult to disentangle different effects of interconnected variables, this study showed that it is possible to isolate single interactions.

The finding that reproductive performance depends to a certain extent on mole cricket occurrence which is in turn affected by the presence of sandy, non-gravelly soils, underlines that habitat selection is of paramount importance for hoopoes. Further conservation actions should include the knowledge about habitat preferences of mole crickets in order to preserve sites with abundant food resources for the hoopoes in Switzerland.

Acknowledgements

I am grateful to Dr. Michael Schaub for his supervision and for his support during the fieldwork and statistical analysis and to Prof. Dr. Raphaël Arlettaz for his co-supervision and for sharing his knowledge about the study species.

Furthermore I would like to thank Thomas Reichlin whose organisation of the fieldwork was extraordinary as were his general working inputs.

I would like to thank all people who helped catching birds, namely Thomas Reichlin, Laura Dafond, Paul Mosimann, Murielle Mermod and Myles Menz. Without their assistance it would not have been possible to capture so many birds. A special thanks goes to Antoine Sierro for showing how to control nest boxes and to the Swiss Ornithological Institute for the material support and the allowance to ring hoopoes.

I am grateful to Alexandre Vogel (Service des Routes et Cours d'Eau, DTEE, Valais) for provision of ground water table maps and information about soil type of the study area. I am also grateful to Fitsum Abadi Gebreselassie and Jean-Pierre Airoldi for providing solutions for statistical problems, to Natalina Signorell for GIS aid, to Olivier Roth for access to the library and to Marcel Moser for IP-support. Garth Fletcher gave very useful information on digital photo-analyses.

Finally, I want to thank Natalie Schäfer and Andreas Sutter for their assistance during funnel pitfall trap installation and control and for their mental support.

References

Arlettaz, R. (1984) Ecologie d'une population de Huppes, *Upupa e. epops*, en Valais: répartition spatiale, biotopes et sites de nidification. *Nos Oiseaux*, **37**, 197-222.

Arlettaz, R., Reichlin, T., Fournier, J., Sierro, A. & Schaub, M. (in prep.) Bridging the gap between conservation research and action: rapid recovery of a hoopoe population after active implementation of corrective, evidence-based recommendations.

Barbraud, C., Weimerskirch, H., Robertson, G. G. & Jouventin, P. (1999) Size-related life history traits: insights from a study of snow petrels (*Pagodroma nivea*). *Journal of Animal Ecology*, **68**, 1179-1192.

Bonser, R. H. C. (1995) Melanin and the abrasion resistance of feathers. *The Condor*, **97**, 590-591.

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.

Burnham, K. P. & Anderson, D. R. (1998) *Model Selection and Inference*. Springer-Verlag, New York.

Burnham, K. P. & Anderson, D. R. (2002) *Model Selection and Multimodel Inference,* Second Edition edn. Springer-Verlag, New York.

Fischer, R.A (1930) *The genetical theory of natural selection*. Claredon Press, Oxford.

Forstmeier, W. (2002) Benefits of early arrival at breeding grounds vary between males. *Journal of Animal Ecology*, **71**, 1-9.

Fournier, J. (1991) *Ecologie d'une population de Huppes fasciées,* Upupa e. epops (L.) *en période de nidification en Valais: Etat de la population, concurrence dans l'occupation des cavités, régime alimentaire, rythme de nourrissage et exploitation du milieu.* Travail de licence, Université de Neuchâtel.

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.

Fugle, G. N., Rothstein, S. I., Osenberg, C. W. & McGinley, M. A. (1984) Signals of status in wintering white-crowned sparrows, *Zonotrichia leucophrys gambelii*. *Animal Behaviour*, **32**, 86-93.

Gil, D. & Gahr, M. (2002) The honesty of bird song: multiple constraints for multiple traits. *Trends in Ecology & Evolution*, **17**, 133-141.

Griggio, M., Serra, L., Licheri, D., Monti, A. & Pilastro, A. (2007) Armaments and ornaments in the rock sparrow: a possible dual utility of a carotenoid-based feather signal. *Behavioral Ecology and Sociobiology*, **61**, 423-433.

Ioset, A. (2007) *The importance of bare ground for terrestrially foraging insectivorous farmland birds: a case study of the endangered Hoopoes* (Upupa epops)*.* Diplomarbeit, Universität Bern.

Jacobs, W. & Renner, M. (1974) *Taschenlexikon zur Biologie der Insekten.* Gustav Fischer Verlag, Stuttgart.

Klomp, H. (1970) Determination of clutch-size in birds: a review. *Ardea*, **58**, 1-124.

Lessells, C. M. & Boag, P. T. (1987) Unrepeatable repeatabilities: a common mistake. *The Auk*, **104**, 116-121.

Loyau, A., Saint Jalme, M. & Sorci, G. (2005) Intra- and Intersexual Selection for Multiple Traits in the Peacock (*Pavo cristatus*). *Ethology*, **111**, 810-820.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A. & Langtimm, C. A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.

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. (1998) Song structure in the Hoopoe (*Upupa epops*) - Strophe length reflects male condition. *Journal für Ornithologie*, **139**, 287-296.

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.

Meijer, T., Daan, S. & Hall, M. (1990) Family planning in the kestrel (*Falco tinnunculus*): the proximate control of covariation of laying date and clutch size. *Behaviour*, **114**, 117-136.

Mermod, M. (2008) *Key ecological features for the persistence of an endangered migratory woodpecker of farmland, the wryneck* (Jynx torquilla). Diplomarbeit, Universität Bern.

Nudds, T. D. & Kaminski, R. M. (1984) Sexual size dimorphism in relation to resource partitioning in North American dabbling ducks. *Canadian Journal of Zoology*, **62**, 2009-2012.

Palmer, A. R. & Strobeck, C. (1986) Fluctuating Asymmetry: Measurement, Analysis, Patterns. *Annual Review of Ecology and Systematics*, **17**, 391-421.

Schaad, M. (2002) *Influence of weather conditions on chick provisioning activity in the Hoopoe* (Upupa e. epops). Diplomarbeit, Universität Bern.

Stearns, S. C. (1976) Life-history tactics: a review of the ideas. *The Quarterly Review of Biology*, **51**, 3-47.

Svensson, L. (1992) *Identification Guide to European Passerines*, 4th, rev. and enlarged edition edn. Lars Svensson, Stockholm.

van Oort, H., Otter, K. A., Fort, K. T. & McDonell, Z. (2007) Habitat, dominance, and the phenotypic quality of male Black-capped Chickadees. *The Condor*, **109**, 88-96.

Verhulst, S., van Balen, J. H. & Tinbergen, J. M. (1995) Seasonal decline in reproductive success of the great tit: variation in time or quality? *Ecology*, **76**, 2392-2403.

Verhulst, S., Perrins, C. M. & Riddington, R. (1997) Natal dispersal of Great Tits in a patchy environment. *Ecology*, **78**, 864-872.

White, G. C. & Burnham, K. P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, S120-139.

Tables

Table 1: Loadings of the first three principal components from a PCA of six morphological variables conducted for female (n= 83) and male (n = 74) hoopoes separately.

	PC 1		PC 2		PC 3	
variables	♂	♀	♂	♀	♂	♀
Tarsus length	-0.391	-0.14	0.486	0.677	-0.4	-0.123
Crest length	-0.421	-0.451	-0.117	0.246	0.483	0.46
Bill length	-0.336	-0.293	0.166	0.446	0.682	0.248
Primary P5 length	-0.444	-0.574	-0.461	-0.295	-0.203	-0.216
1st tail feather length	-0.414	-0.563	-0.507	-0.382	-0.263	0.047
weight	-0.433	-0.212	0.503	0.223	-0.177	-0.813
% variance accounted for	0.337	0.341	0.192	0.214	0.172	0.179

Table 2: Model selection summary for the probability of mole cricket gallery occurrence (ψ) and their detection (p) evaluated with occupancy models for 111 plots. Given are differences in AIC values between the best and the current model (ΔAICc), AIC weights (AICw) number of estimated parameters (K) and the deviance.

Explanatory parameters: (.) = constant, t = time dependent, gr = grass height, bg = amount of bare ground, soil = soil categories 1-5, water = water table height, fruit = orchard fruit type, age = orchard age, sandy and other = sandy, non-gravelly soil category versus all other categories.

Model	ΔAICc	AICw	K	Deviance
p(gr + bg) ψ(sandy and other)	0	0.43	5	263.79
p(gr+ bg) ψ(sandy and other+ water)	1.93	0.16	6	263.48
p(gr) ψ(sandy and other)	3	0.1	4	268.98
p(gr + bg) ψ(.)	3.2	0.09	4	269.18
p(bg) ψ(sandy and other)	4.24	0.05	4	270.23
p(gr) ψ(sandy and other + water)	4.91	0.04	5	268.7
p(gr + bg) ψ(water)	5.26	0.03	5	269.05
p(gr + bg) ψ(soil)	5.98	0.02	8	262.92
p(bg) ψ(sandy and other + water)	6.14	0.02	5	269.93
p(gr) ψ(.)	6.34	0.02	3	274.48
p(bg) ψ(.)	7.49	0.01	3	275.63
p(gr + bg) ψ(sandy and other + water)	7.92	0.01	9	262.5
p(gr) ψ(water)	8.38	0.01	4	274.37
p(gr) ψ(soil)	8.84	0.01	7	268.11
p(.) ψ(sandy and other)	9.09	0	3	277.23
p(bg) ψ(water)	9.52	0	4	275.5
p(bg) ψ(soil)	10.07	0	7	269.35
p(gr) ψ(soil + water	10.77	0	8	267.72
p(.) ψ(sandy and other + water)	10.97	0	4	276.95
p(bg) ψ(soil + water)	11.98	0	8	268.93
p(.) ψ(.)	12.5	0	2	282.75
p(.) ψ(water)	14.5	0	3	282.64
p(.) ψ(soil)	14.8	0	6	276.35
p(.) ψ(soil + water)	16.69	0	7	275.96

Table 3: Model selection summary of clutch size of hoopoe females using general linear mixed models (n = 53). In a first step breeding attempt and hatching date, in a second step the 3 principal component scores (morphology), and in the final step the age and mole cricket index (MCI) were modelled. The ΔAIC, the models deviance (Deviance) and the number of parameters estimated (K) are given. The best models (ΔAIC < 1.5) within the three steps are highlighted.

	Variables									
Model	Breeding attempt	Hatching date	PC1	PC2	PC3	age	MCI	ΔAIC	Dev.	K
1	**0**	**1**	**1**	**1**	**1**	**1**	**1**	**0**	**5.15**	**8**
2	**1**	**0**	**1**	**1**	**1**	**1**	**1**	**0.35**	**5.5**	**8**
3	**0**	**0**	**1**	**1**	**1**	**1**	**1**	**0.61**	**7.76**	**7**
4	1	1	1	1	1	1	1	1.9	5.05	9
5	**0**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	**5.64**	**5**
6	**1**	**0**	**0**	**0**	**0**	**1**	**1**	**1.39**	**7.03**	**5**
7	0	1	0	1	0	1	1	1.52	5.16	6
8	0	0	0	0	0	1	1	1.71	9.35	4
9	0	1	0	0	1	1	1	1.98	5.62	6
10	0	1	1	0	0	1	1	1.99	5.63	6
11	1	0	0	1	0	1	1	2.18	5.82	6
12	0	0	0	1	0	1	1	2.4	8.04	5
13	1	0	1	0	0	1	1	2.93	6.57	6
14	1	0	0	0	1	1	1	3.23	6.87	6
15	0	0	1	0	0	1	1	3.28	8.92	5
16	0	1	1	1	0	1	1	3.51	5.15	7
17	0	1	0	1	1	1	1	3.51	5.15	7
18	0	0	0	0	1	1	1	3.6	9.24	5
19	1	0	1	1	0	1	1	3.9	5.54	7
20	0	1	1	0	1	1	1	3.97	5.61	7
21	1	0	0	1	1	1	1	4.13	5.77	7
22	0	0	1	1	0	1	1	4.13	7.77	6
23	0	0	0	1	1	1	1	4.37	8.01	6
24	1	0	1	0	1	1	1	4.83	6.47	7
25	0	0	1	0	1	1	1	5.21	8.85	6
26	0	1	1	1	1	1	1	5.51	5.15	8
27	1	0	1	1	1	1	1	5.86	5.5	8
28	0	0	1	1	1	1	1	6.12	7.76	7
29	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**5.79**	**3**
30	1	0	0	0	0	0	0	1.68	7.47	3
31	0	1	0	0	0	1	0	1.87	5.66	4
32	0	1	0	0	0	0	1	1.97	5.76	4
33	0	0	0	0	0	0	0	2.23	10.02	2
34	1	0	0	0	0	0	1	3.27	7.06	4
35	1	0	0	0	0	1	0	3.58	7.37	4
36	0	1	0	0	0	1	1	3.85	7.03	5
37	1	0	0	0	0	1	1	5.24	7.03	5

Table 4: Model selection summary of clutch size of hoopoe males using general linear mixed models (n = 35). In a first step breeding attempt and hatching date, in a second step the 3 principal component scores (morphology), and in the final step the age and mole cricket index (MCI) were modelled. The ΔAIC, the models deviance (Deviance) and the number of parameters estimated (K) are given. The best models (ΔAIC < 1.5) within the three steps are highlighted.

	Variables									
Model	Breeding attempt	Hatching date	PC1	PC2	PC3	age	MCI	ΔAIC	Dev.	K
1	**0**	**1**	**1**	**1**	**1**	**1**	**1**	**0.00**	**3.10**	**8**
2	**0**	**0**	**1**	**1**	**1**	**1**	**1**	**0.34**	**5.44**	**7**
3	1	0	1	1	1	1	1	1.74	4.84	8
4	1	1	1	1	1	1	1	1.99	3.09	9
5	**0**	**1**	**0**	**0**	**0**	**1**	**1**	**0.00**	**3.19**	**5**
6	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0.96**	**6.15**	**4**
7	0	1	0	0	1	1	1	1.91	3.10	6
8	0	1	1	0	0	1	1	2.00	3.19	6
9	0	1	0	1	0	1	1	2.00	3.19	6
10	0	0	0	0	1	1	1	2.58	5.77	5
11	0	0	0	1	0	1	1	2.75	5.95	5
12	0	0	1	0	0	1	1	2.86	6.05	5
13	0	1	1	0	1	1	1	3.91	3.10	7
14	0	1	0	1	1	1	1	3.91	3.10	7
15	0	1	1	1	0	1	1	3.99	3.18	7
16	0	0	1	0	1	1	1	4.37	5.56	6
17	0	0	0	1	1	1	1	4.42	5.61	6
18	0	0	1	1	0	1	1	4.68	5.87	6
19	0	1	1	1	1	1	1	5.91	3.10	8
20	0	0	1	1	1	1	1	6.25	5.44	7
21	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0.00**	**3.20**	**3**
22	0	0	0	0	0	0	0	1.54	6.24	2
23	0	1	0	0	0	1	0	1.99	3.19	4
24	0	1	0	0	0	0	1	1.99	3.20	4
25	0	0	0	0	0	0	1	2.96	6.16	3
26	0	0	0	0	0	1	0	3.01	6.21	3
27	0	1	0	0	0	1	1	3.99	3.19	4
28	0	0	0	0	0	1	1	4.95	6.15	4

Table 5: Model selection summary of number of fledglings of hoopoe females using general linear mixed models (n = 73). In a first step breeding attempt and hatching date, in a second step the 3 principal component scores (morphology), and in the final step the age and mole cricket index (MCI) were modelled. Additionally, fixed weather parameters (rainfall and temperature) were included in the models. The ΔAIC, the models deviance (Deviance) and the number of parameters estimated (K) are given. The best models (ΔAIC < 1.5) within the three steps are highlighted.

	Variables									
Model	Breeding attempt	Hatching date	PC1	PC2	PC3	age	MCI	ΔAIC	Dev.	K
1	**0**	**1**	**1**	**1**	**1**	**1**	**1**	**0**	**93.57**	**12**
2	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**0.3**	**91.89**	**13**
3	1	0	1	1	1	1	1	1.8	95.41	12
4	0	0	1	1	1	1	1	5.4	101	11
5	**0**	**1**	**0**	**0**	**1**	**1**	**1**	**0**	**93.88**	**10**
6	**0**	**1**	**0**	**0**	**0**	**1**	**1**	**0.6**	**96.5**	**9**
7	**1**	**1**	**0**	**0**	**1**	**1**	**1**	**0.9**	**92.83**	**11**
8	0	1	1	0	1	1	1	1.7	93.6	11
9	1	1	0	0	0	1	1	1.8	96.5	10
10	0	1	0	1	1	1	1	1.9	93.82	11
11	1	1	1	0	1	1	1	2	91.91	12
12	0	1	1	0	0	1	1	2.4	96.3	10
13	0	1	0	1	0	1	1	2.5	96.43	10
14	1	1	0	1	1	1	1	2.9	92.75	12
15	1	1	1	0	0	1	1	3.2	95.06	11
16	1	1	0	1	0	1	1	3.7	95.62	11
17	0	1	1	1	1	1	1	3.7	93.57	12
18	1	1	1	1	1	1	1	4	91.89	13
19	0	1	1	1	0	1	1	4.4	96.26	11
20	1	1	1	1	0	1	1	5.1	95.02	12
21	**0**	**1**	**0**	**0**	**1**	**0**	**0**	**0**	**94.33**	**8**
22	**1**	**1**	**0**	**0**	**1**	**0**	**0**	**1**	**93.3**	**9**
23	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**1.2**	**97.45**	**7**
24	0	1	0	0	1	0	1	1.6	93.88	9
25	0	1	0	0	1	1	0	2	94.32	9
26	0	1	0	0	0	0	1	2.3	96.58	8
27	1	1	0	0	1	0	1	2.5	92.84	10
28	0	1	0	0	0	1	0	2.9	97.24	8
29	1	1	0	0	1	1	0	3	93.3	10
30	0	1	0	0	1	1	1	3.6	93.88	10
31	0	1	0	0	0	1	1	4.2	96.5	9
32	1	1	0	0	1	1	1	4.5	92.83	11
33	0	0	0	0	0	0	0	6.9	105.2	6

Table 6: Model selection summary of number of fledglings of hoopoe males using general linear mixed models (n = 54). In a first step breeding attempt and hatching date, in a second step the 3 principal component scores (morphology), and in the final step the age and mole cricket index (MCI) were modelled. Additionally, fixed weather parameters (rainfall and temperature) were included in the models. The ΔAIC, the models deviance (Deviance) and the number of parameters estimated (K) are given. The best models (ΔAIC < 1.5) within the three steps are highlighted.

	Variables									
Model	Breeding attempt	Hatching date	PC1	PC2	PC3	age	MCI	ΔAIC	Dev.	K.
1	**0**	**1**	**1**	**1**	**1**	**1**	**1**	**0.00**	**51.89**	**12**
2	1	1	1	1	1	1	1	1.82	51.71	13
3	0	0	1	1	1	1	1	5.80	59.69	11
4	1	0	1	1	1	1	1	7.48	59.37	12
5	**0**	**1**	**0**	**0**	**0**	**1**	**1**	**0.00**	**52.14**	**9**
6	0	1	1	0	0	1	1	1.80	51.94	10
7	0	1	0	0	1	1	1	1.98	52.12	10
8	0	1	0	1	0	1	1	1.99	52.13	10
9	0	1	1	0	1	1	1	3.76	51.90	11
10	0	1	1	1	0	1	1	3.78	51.92	11
11	0	1	0	1	1	1	1	3.97	52.11	11
12	0	1	1	1	1	1	1	5.75	51.89	12
13	**0**	**1**	**0**	**0**	**0**	**1**	**0**	**0.00**	**52.85**	**8**
14	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**1.15**	**56.00**	**7**
15	**0**	**1**	**0**	**0**	**0**	**1**	**1**	**1.29**	**52.14**	**9**
16	0	1	0	0	0	0	1	1.77	54.62	8
17	0	0	0	0	0	0	0	8.25	65.10	6

Table 7: Comparison of candidate models (conducted using a general linear mixed model; n = 16) explaining clutch size with female and male characteristics and habitat. Hatching date, individual age, mole cricket index (MCI), PC1-3 scores, irregularity of tail stripe and fluctuating asymmetry of primary P5 (FA) were included (1) as explanatory variables. The dAIC (ΔAIC), the models deviance (Dev.) and the number of parameters estimated (K.) The best models (ΔAIC < 1.5) within the three steps are highlighted.

	variables										
Model	Hatching date	PC1	PC2	PC3	FA	tail stripe	age	MCI	ΔAIC	Dev.	K.
1	**0**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**0.00**	**1.26**	**9**
2	1	1	1	1	1	1	1	1	1.55	0.81	10
3	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0.00**	**2.27**	**4**
4	0	0	0	0	1	0	1	1	1.68	1.95	5
5	0	0	0	1	0	0	1	1	1.71	1.98	5
6	0	0	1	0	0	0	1	1	1.72	1.99	4
7	0	1	0	0	0	0	1	1	1.98	2.25	5
8	0	0	0	0	0	1	1	1	2.00	2.27	5
9	0	0	1	0	1	0	1	1	3.32	1.59	6
10	0	0	0	1	1	0	1	1	3.36	1.63	6
11	0	0	1	1	0	0	1	1	3.55	1.82	6
12	0	1	0	1	0	0	1	1	3.59	1.86	6
13	0	1	0	0	1	0	1	1	3.67	1.94	6
14	0	1	1	0	0	0	1	1	3.68	1.95	6
15	0	0	0	0	1	1	1	1	3.68	1.95	6
16	0	0	1	0	0	1	1	1	3.70	1.97	6
17	0	0	0	1	0	1	1	1	3.70	1.97	6
18	0	1	0	0	0	1	1	1	3.98	2.25	6
19	0	0	1	1	1	0	1	1	5.14	1.41	7
20	0	1	0	1	1	0	1	1	5.27	1.55	7
21	0	1	1	0	1	0	1	1	5.30	1.57	7
22	0	0	1	0	1	1	1	1	5.31	1.58	7
23	0	0	0	1	1	1	1	1	5.36	1.63	7
24	0	1	1	1	0	0	1	1	5.43	1.70	7
25	0	1	0	1	0	1	1	1	5.54	1.81	7
26	0	1	1	0	0	1	1	1	5.64	1.91	7
27	0	1	0	0	1	1	1	1	5.67	1.94	7
28	0	1	1	1	1	0	1	1	7.06	1.33	8
29	0	0	1	1	1	1	1	1	7.12	1.39	8
30	0	0	1	1	0	1	1	1	7.18	1.45	7
31	0	1	0	1	0	1	1	1	7.25	1.52	8
32	0	1	1	0	1	1	1	1	7.28	1.55	8
33	0	1	1	1	0	1	1	1	7.33	1.60	8
34	0	1	1	1	1	1	1	1	8.99	1.26	9
35	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**	**2.28**	**2**
36	0	0	0	0	0	0	1	0	1.99	2.27	3
37	0	0	0	0	0	0	0	1	2.00	2.28	3
38	0	0	0	0	0	0	1	1	3.99	2.27	4

Table 8: Comparison of candidate models (conducted using a general linear mixed model; n = 30) explaining number of fledglings with female and male characteristics and habitat. Hatching date, individual age, mole cricket index (MCI), PC1-3 scores, irregularity of tail stripe, fluctuating asymmetry of primary P5 (FA) were included (1) as explanatory variables. Weather variables (t0, t3, r0, r1) were included in every model. The dAIC (ΔAIC), the models deviance (Dev.) and the number of parameters estimated (K.) The best models (ΔAIC < 1.5) within the three steps are highlighted.

	variables										
Model	Hatching date	PC1	PC2	PC3	FA	tail stripe	age	MCI	ΔAIC	Dev.	K.
1	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**0.00**	**32.34**	**14**
2	0	1	1	1	1	1	1	1	1.69	36.03	13
3	**1**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**0.00**	**33.96**	**9**
4	**1**	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**0.76**	**32.72**	**10**
5	1	0	1	0	0	0	1	1	1.53	33.49	10
6	1	1	0	0	0	0	1	1	1.66	33.62	10
7	1	0	0	1	0	0	1	1	1.80	33.76	10
8	1	0	0	0	1	0	1	1	2.00	33.96	10
9	1	0	0	0	1	1	1	1	2.57	32.53	11
10	1	0	1	0	0	1	1	1	2.69	32.65	11
11	1	1	0	0	0	1	1	1	2.70	32.66	11
12	1	0	0	1	0	1	1	1	2.73	32.69	11
13	1	1	1	0	0	0	1	1	3.05	33.01	11
14	1	0	1	1	0	0	1	1	3.45	33.41	11
15	1	0	1	0	1	0	1	1	3.49	33.45	11
16	1	1	0	1	0	0	1	1	3.50	33.46	11
17	1	1	0	0	1	0	1	1	3.65	33.61	11
18	1	0	0	1	1	0	1	1	3.79	33.75	11
19	1	0	0	0	1	1	1	1	4.45	32.41	12
20	1	0	0	1	1	1	1	1	4.52	32.48	12
21	1	1	1	0	0	1	1	1	4.56	32.52	12
22	1	1	0	0	1	1	1	1	4.56	32.52	12
23	1	1	0	1	0	1	1	1	4.67	32.63	12
24	1	0	1	1	0	1	1	1	4.67	32.63	12
25	1	1	1	1	0	0	1	1	5.01	32.97	12
26	1	1	1	0	1	0	1	1	5.05	33.01	12
27	1	0	1	1	1	0	1	1	5.41	33.37	12
28	1	1	0	1	1	0	1	1	5.50	33.46	12
29	1	1	1	0	1	1	1	1	6.40	32.36	13
30	1	0	1	1	1	1	1	1	6.42	32.38	13
31	1	1	0	1	1	1	1	1	6.51	32.47	13
32	1	1	1	1	0	1	1	1	6.55	32.51	13
33	1	1	1	1	1	0	1	1	7.01	32.97	13
34	**1**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0.00**	**34.44**	**8**
35	**1**	**0**	**0**	**0**	**0**	**1**	**1**	**0**	**0.82**	**33.26**	**9**
36	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1.37**	**37.81**	**7**
37	1	0	0	0	0	1	0	0	2.00	36.44	8
38	1	0	0	0	0	0	0	1	2.30	36.74	8
39	0	0	0	0	0	0	0	0	2.33	40.77	6
40	1	0	0	0	0	1	0	1	2.76	35.20	9

Table 9: Model averaged estimates and standard errors of explanatory variables (breeding attempt per season, hatching date, score of PC 3, tail stripe, age mole cricket index [MCI] and weather) as defined by the best models for the different response variables including either male and female separate or combined. "NI" indicates where the explanatory model was not included in the modelling.

	expl. Variables													
	intercept		Breeding attempt		Hatching date		PC3		Tail stripe		age		MCI	
	est.	se	est.	se	est.	se	est.	se	est.	se	est.	se	est.	se
clutch size ♀	2.5290	0.3360	-	-	-0.0030	0.0030	-	-	NI	NI	-	-	-	-
clutch size ♂	2.4890	0.4680	-	-	-0.0030	0.0030	-	-	NI	NI	-	-	-	-
clutch size ♀+♂	2.1030	0.0870	-	-	-	-	-	-	-	-	-	-	-	-
fledglings ♀	1.3360	0.6810	-0.0490	0.0950	-0.0140	0.0060	0.0830	0.0760	NI	NI	-	-	-	-
fledglings ♂	3.5420	0.8150	NI	NI	-0.0190	0.0050	-	-	NI	NI	-0.1490	0.1640	0.2770	0.5050
fledglings ♀+♂	3.7300	1.8220	NI	NI	-0.0150	0.0070	-	-	0.0060	0.0100	-0.0940	0.0800	-	-

Figure captions

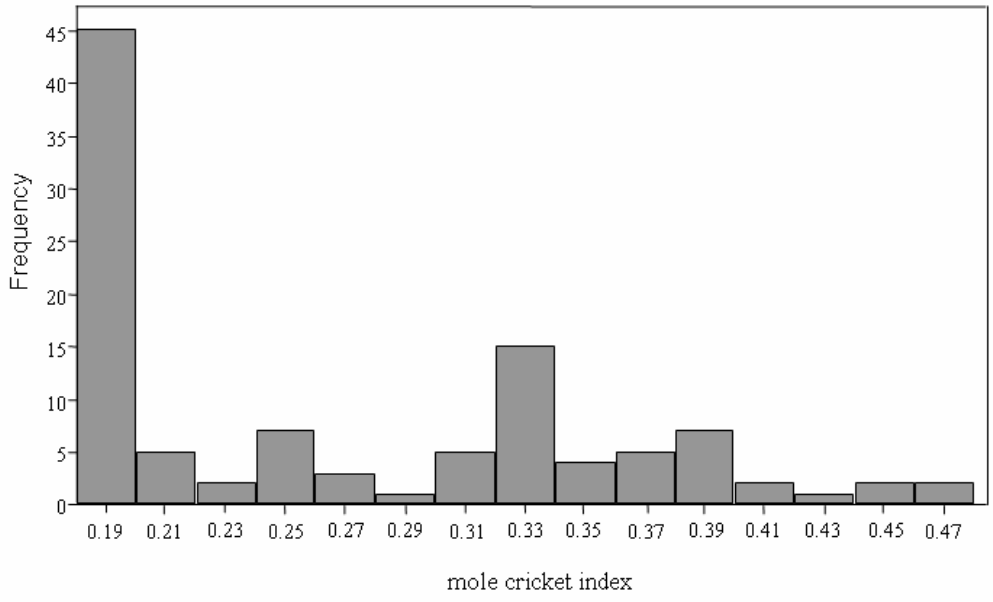
Figure 1: Tail feathers of different hoopoes. Pictures 1-4 show individuals with varying irregularity of the tail stripe from (1) very regular (4.28%) to (4) very irregular (29.83%). Picture 5 demonstrates the methodology of measuring the irregularity of tail stripe. The grey polygon represents the "idealized tail stripe". Areas which deviate from this polygon (white areas and black parts) are shown. The sum of these areas is used as measure of irregularity.

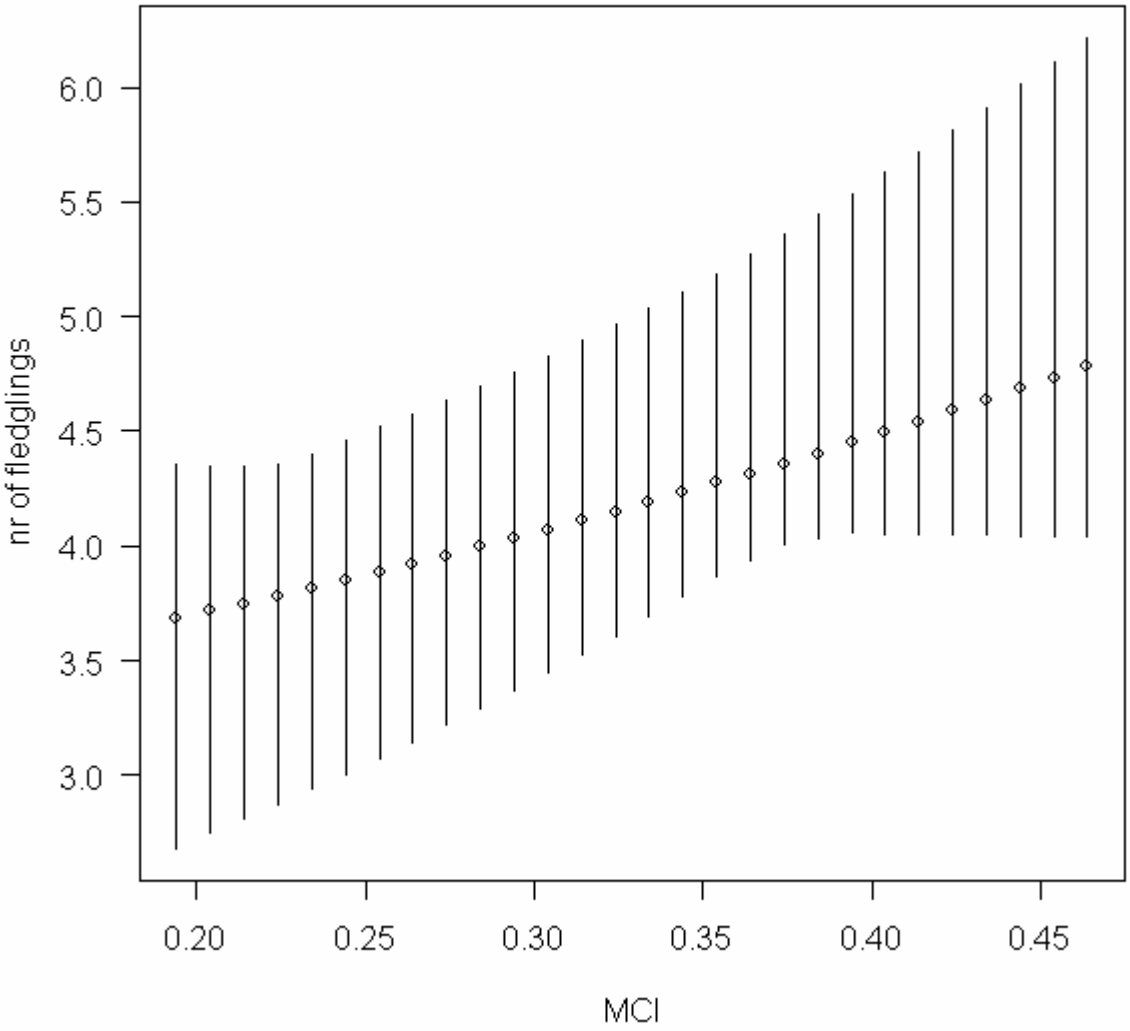
Figure 2: Frequency distribution of mole cricket index obtained for all homeranges, with at least one soil sample (n = 106).

Figure 3: Predictive graph of the relation between the mole cricket index (MCI) and the number of fledglings of the male parent. The three best models from Table 6 were included, keeping the effect of hatching date and age constant (mean). Vertical bars represent the 95% confidence interval.

Figures

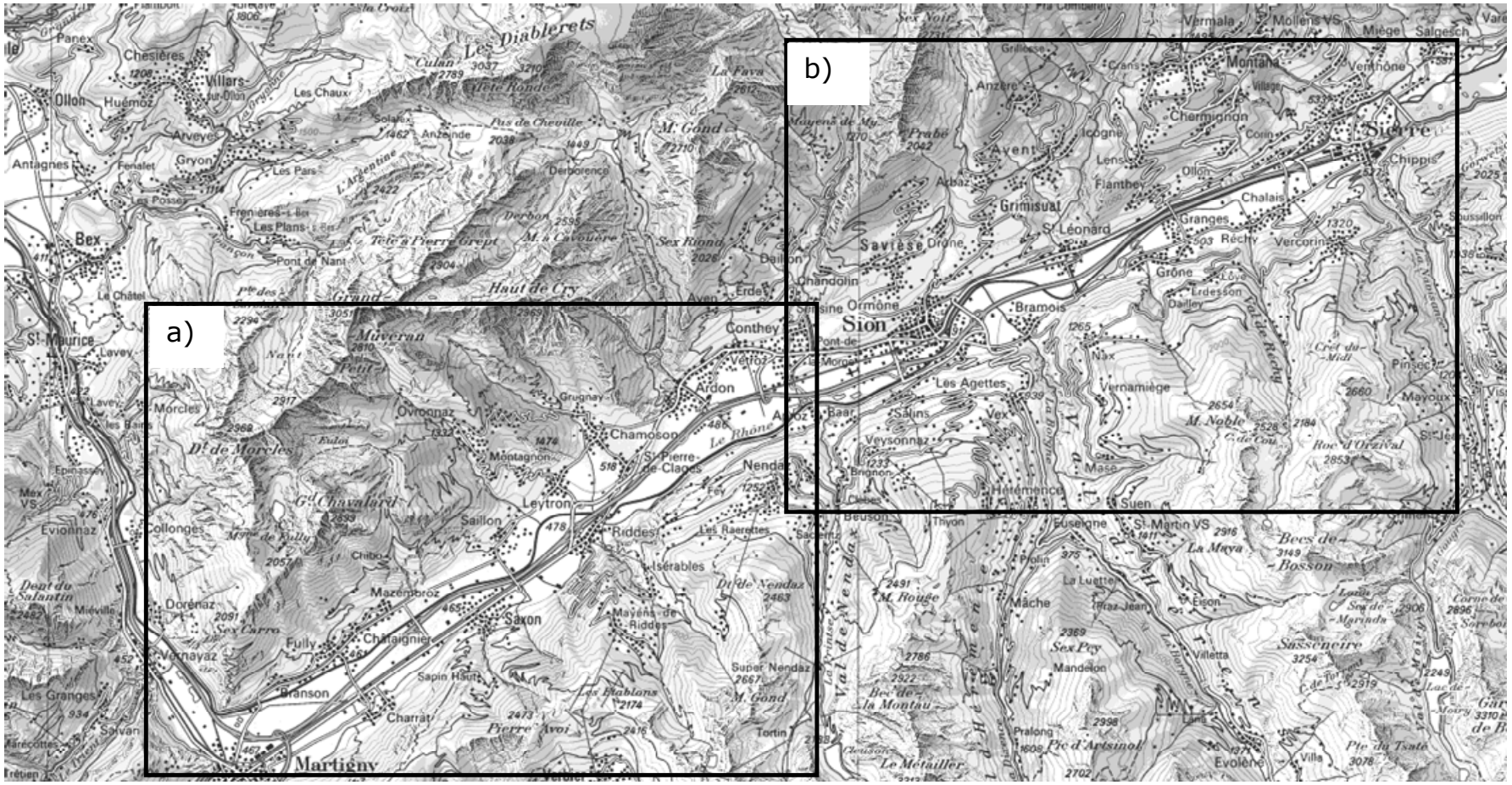
(1)
(2)
(3)
(4)
(5)
a
b


Frequency
45
40
35
30
25
20
15
10
5
0
0.19
0.21
0.23
0.25
0.27
0.29
0.31
0.33
0.35
0.37
0.39
0.41
0.43
0.45
0.47
mole cricket index


nr of fledglings
6.0
5.5
5.0
4.5
4.0
3.5
3.0
0.20
0.25
0.30
0.35
0.40
0.45
MCI

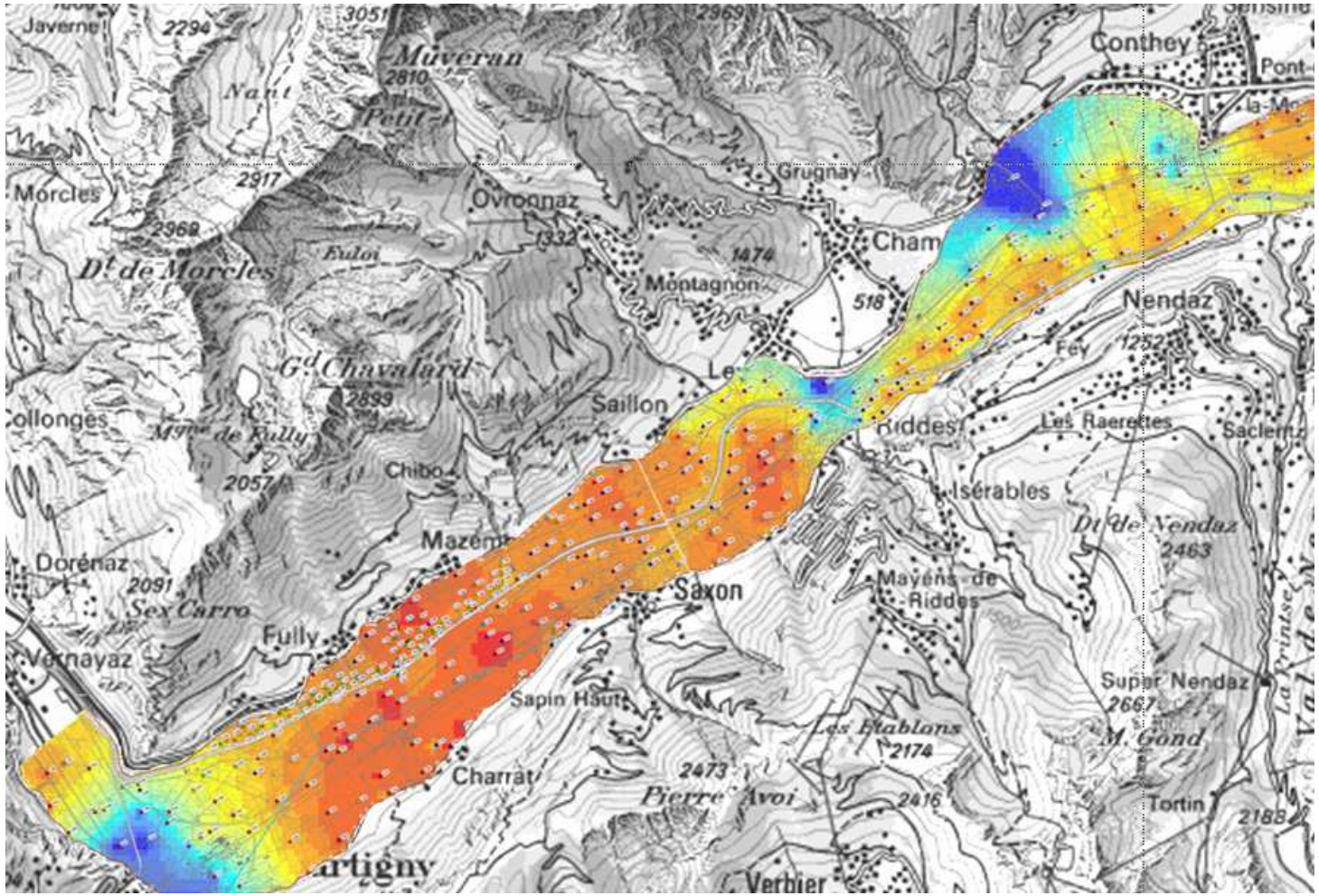
Appendix

Appendix 1: Map of the study area. For a better view, following maps are partitioned into two parts designated here by black frames.

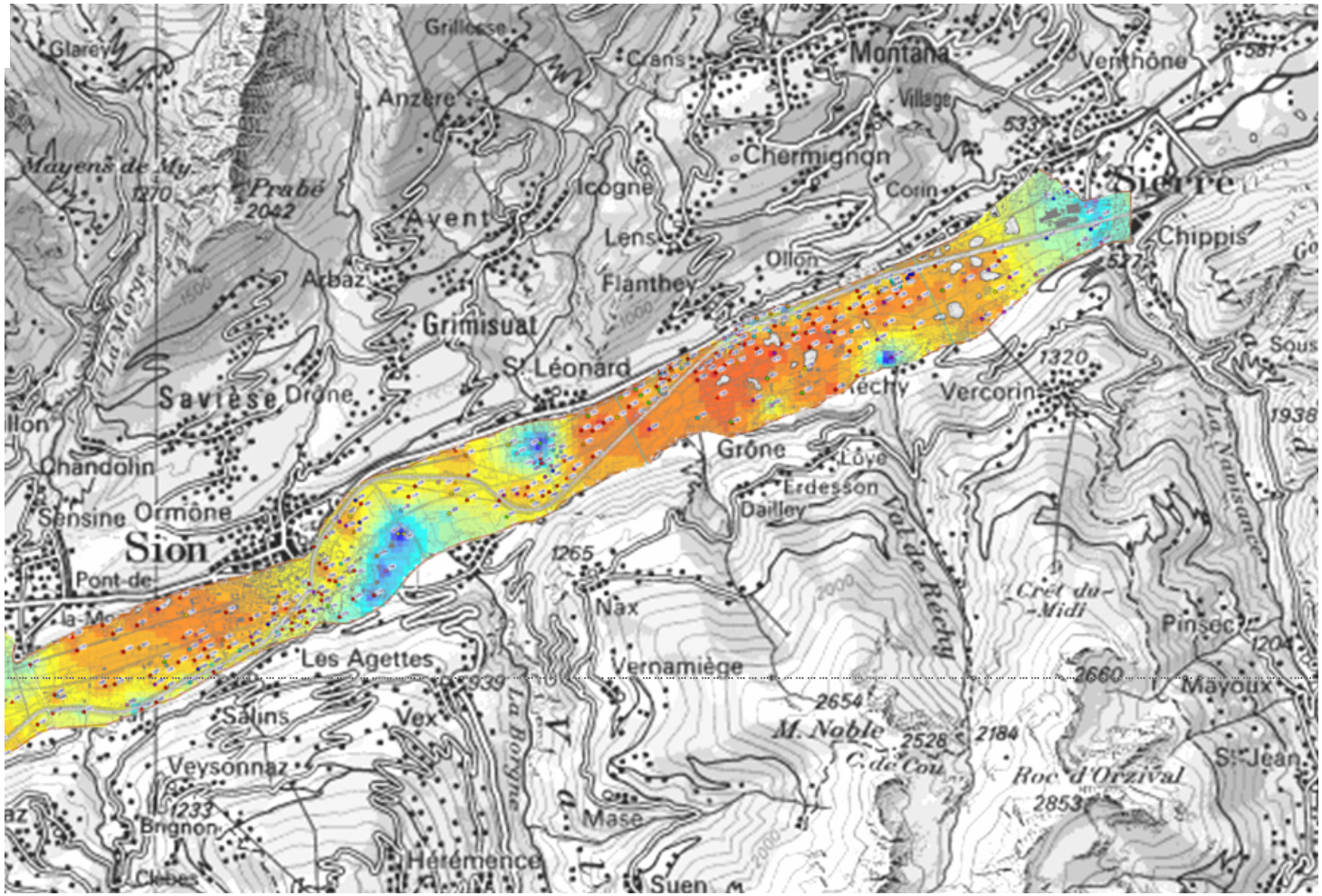


Appendix 2: Maps of water table levels provided by Service des Routes et Cours d'Eau, Canton du Valais. Water table levels range from 0.5 m (dark red) to 8 m (dark blue) below soil surface.

a)

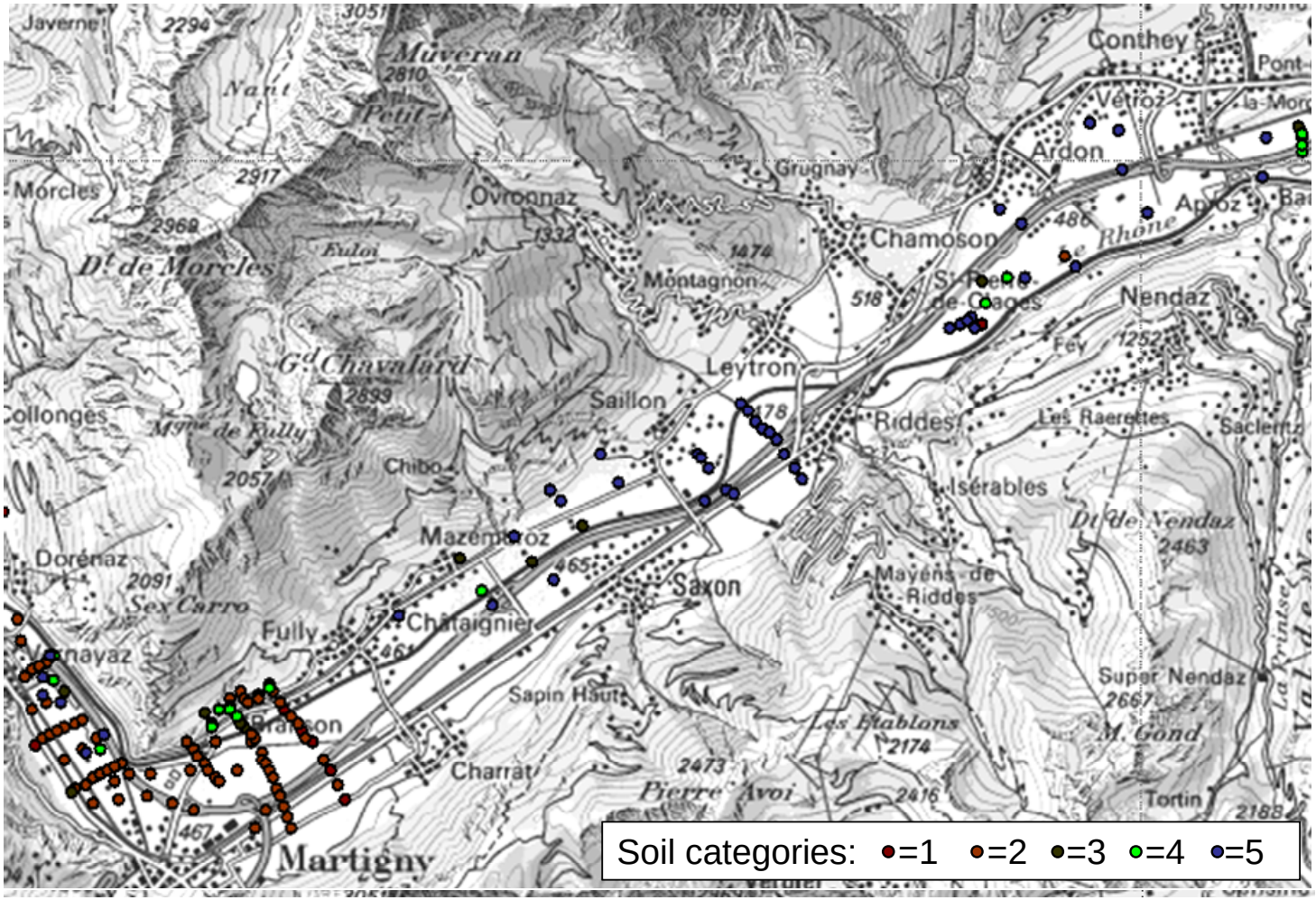


b)

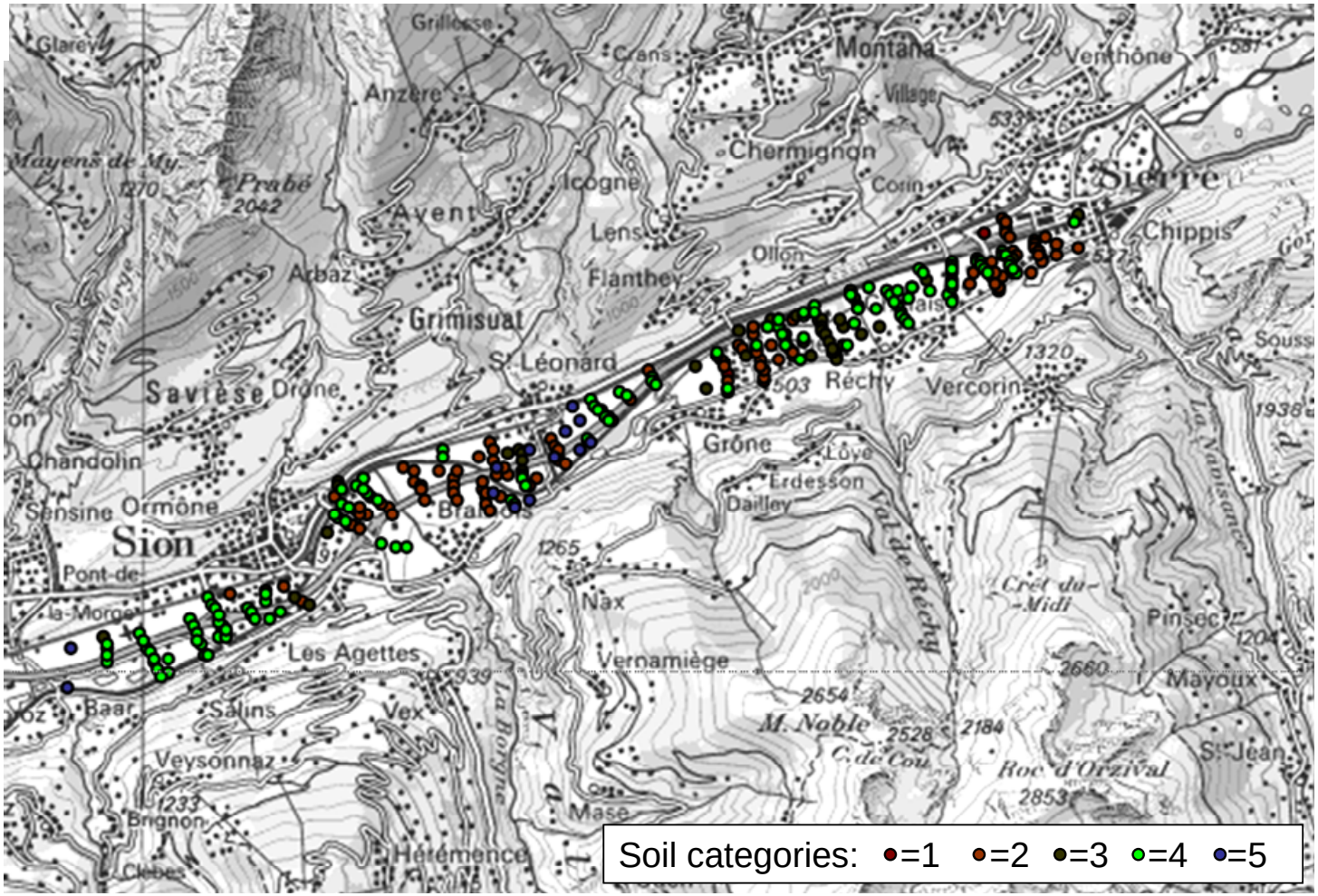

Glarey
Grillesse
Crans
Montana
Venthône
Anzère
Village
Chermignon
Mayens de My
1270
Prabé
2042
Icogne
Corin
Sierre
Avent
Lens
Chippis
Ollon
Arbaz
Flanthey
Grimisuat
St-Léonard
Savièse
Drône
Réchy
Vercorin
1320
1938
Chandolin
Grône
Löye
Erdesson
Dailley
Sensine
Ormône
Sion
1265
Nax
Pont-de-
Crêt du-
-Midi
Pinsec
Les Agettes
Vernamiège
2660
Mayoux
2654
M. Noble
2528
2184
Salins
Vex
St-Jean
Veysonnaz
Roc d'Orzival
2853
1233
Brignon
Mase
Hérémence
Clèbes
Suen

Appendix 3: Map showing the distribution of the 5 soil categories. The soil category preferred by mole crickets (sandy, non-gravelly soil) is shown in bright green. See Appendix 1 for detailed information about soil categories.

a)



b)


Soil categories: =1 =2 =3 =4 =5
Sierre
Montana
Chermignon
Icogne
Lens
Flanthey
Ollon
Chippis
Vercorin
Réchy
Grône
Sion
Grimisuat
Savièse
Arbaz
Ayent
Anzère
Nax
Vernamiège
Les Agettes
Salins
Vex
Veysonnaz
Mayoux
Pinsec
Val de Réchy
La Borgne
La Navisence

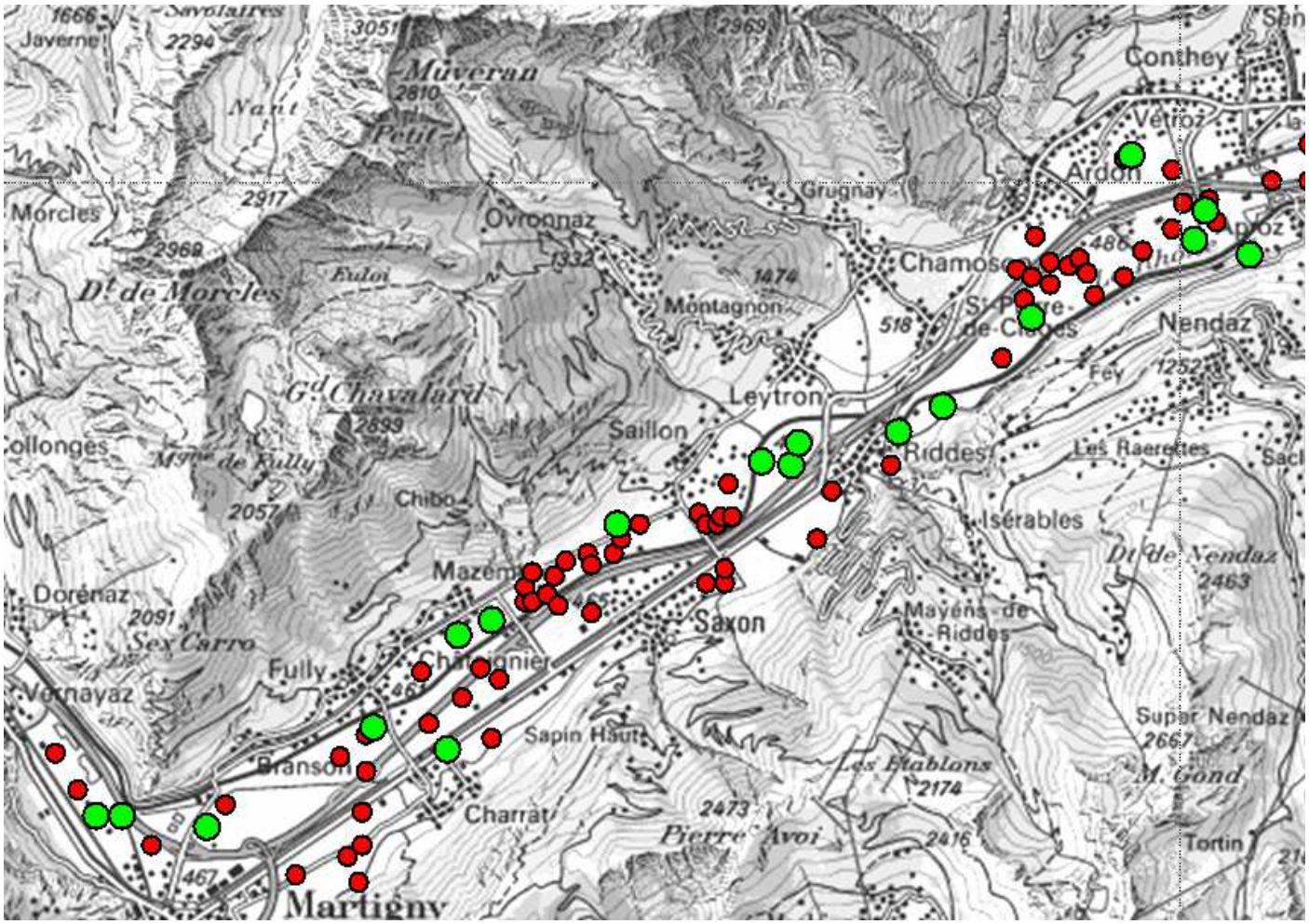
Appendix 4: Categories of soil types defined by the Service des Routes et Cours d'Eau, Département des Transports de l'Environnement, Canton du Valais, and the new categories defined and used in this study.

soil type	category
silt	1
silt, clayey and little sandy	
silt, gravelly	
silt, partially sandy and clayey	
silt, partially sandy	
silt, sandy and little clayey	
silt, sandy with stones	
silt, sandy with some gravel	
silt, sandy with pebbles	
silt, sandy with gravel and pebbles	
silt, sandy with gravel and some pebbles	
silt, sandy with presence of clay	
silt, sandy gravelly	
silt,sandy gravelly with presence of clay	
silt, sandy gravelly with stones and organic material	
silt, sandy and little clayey, becoming more and more silty with presence of pebbles	
silt, sandy and little gravelly	
silt, sandy and little gravelly and pebbly	
silt, sandy-gravelly	
silt, sandy-gravelly with presence of clay	
silt, very little sandy	
silt, very little sandy with gravel and pebbles	
silt, very little sandy and very gravelly	
silt, more or less sandy	2
silt, sandy	
silt, sandy with deposits of grey- beige bosk	
silt, sandy with radix	
silt, sandy brown	
silt, sandy, becoming more and more fine	
silt, sandy with radix and organic material	
silt, sandy with organic material	
silt, very sandy	
blocks with stones accompagned by silty sand	3
gravel, sandy and silty	
gravel, sandy and little silty	
sand, with pebbles	
sand, fine with pebbles	
sand, silty and very gravelly with pebbles	
sand, silty and with pebbles	
sand, silty with gravel	
sand, silty with gravel and pebbles	
sand, silty with organic material and some pebbles	
sand, silty with some gravels	
sand, silty with some gravels and rare organic material	
sand, silty and gravelly	
sand, silty and gravelly with some pebbles	
sand, silty and gravelly with radix	
sand, silty and partially gravelly	
sand, little silty with pebbles	

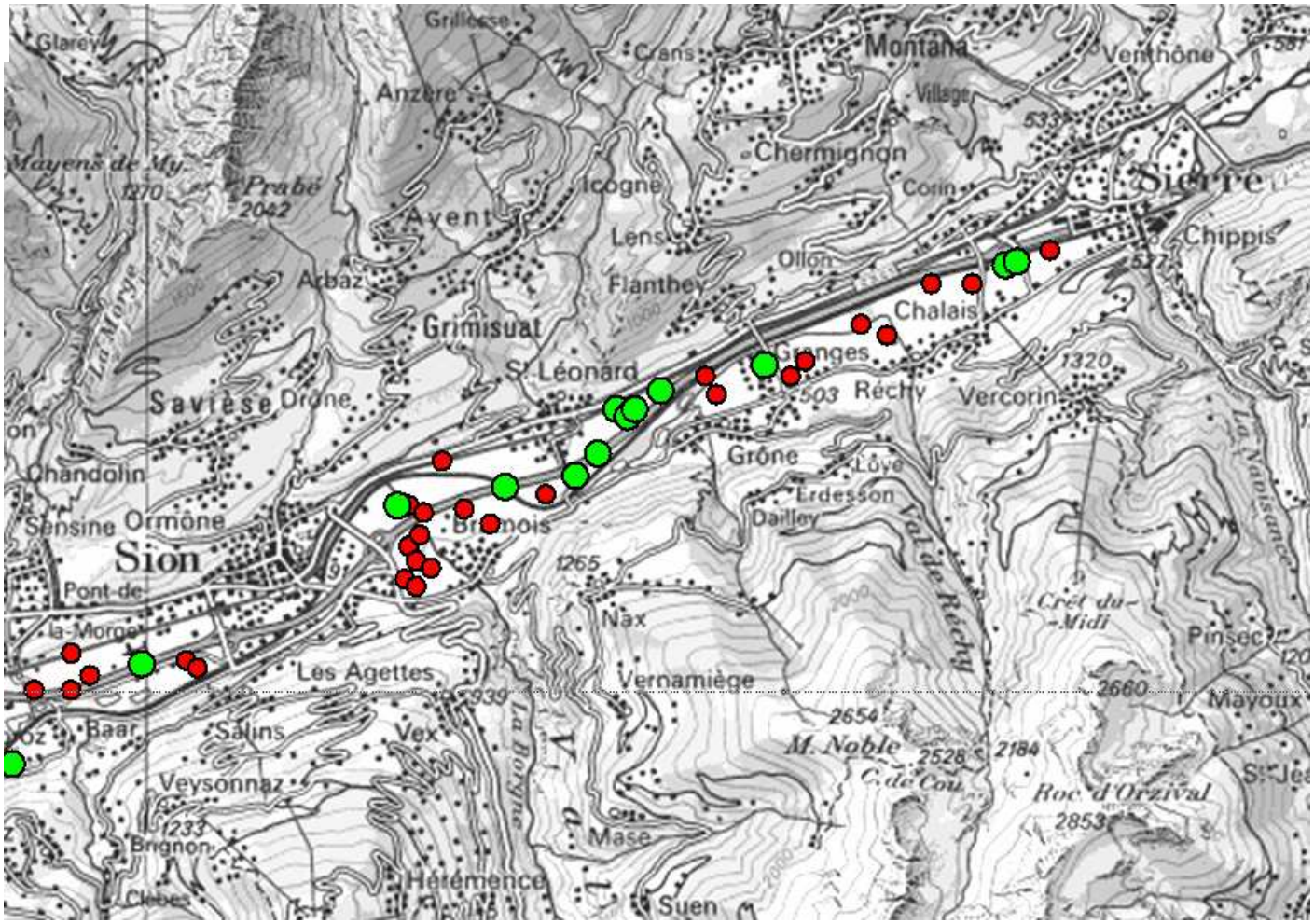
sand, little silty with gravel	
sand, little silty with garvel and pebbles	
sand, little silty and gravey	
sand, little silty and gravelly with pebbles	
sand, little silty and gravelly becoming more and more gravelly	
sand, little silty and very gravelly	
sand, fine and silty	4
sand, fine and little silty	
sand, fin with bosk between 0.5 and 0.6 m	
sand, silty	
sand, silty with sand little silty	
sand, silty becoming more and more silty	
sand, silty becoming more and more sandy	
sand, little silty	
sand, little silty with organic material	
sand, very fine	
sand, very silty	
sand, verly little silty	
vegetal soil	5
vegetal soil, gravelly	
vegetal soil, silty	
vegetal soil, sandy	
vegetal soil, sandy with radix and organic material	
vegetal soil, sandy-silty	
vegetal soil, sandy-silty with organic material	

Appendix 5: Map showing the location of plots checked for mole cricket gallery presence. Red, small circles represent plots where no galleries were detected during the 5 consecutive visits, whereas green, large circles correspond to plots where galleries were detected at least once.

a)

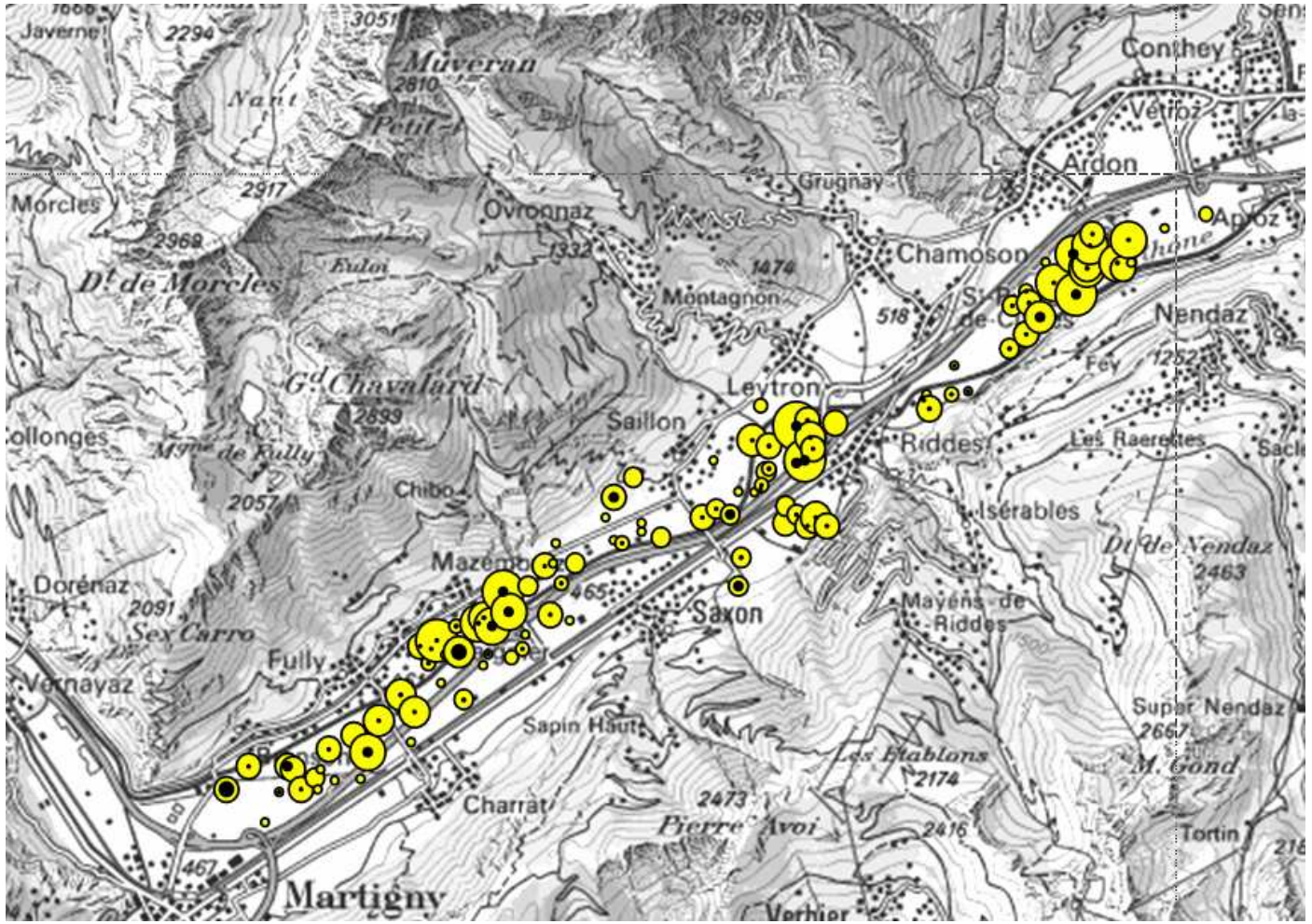


b)

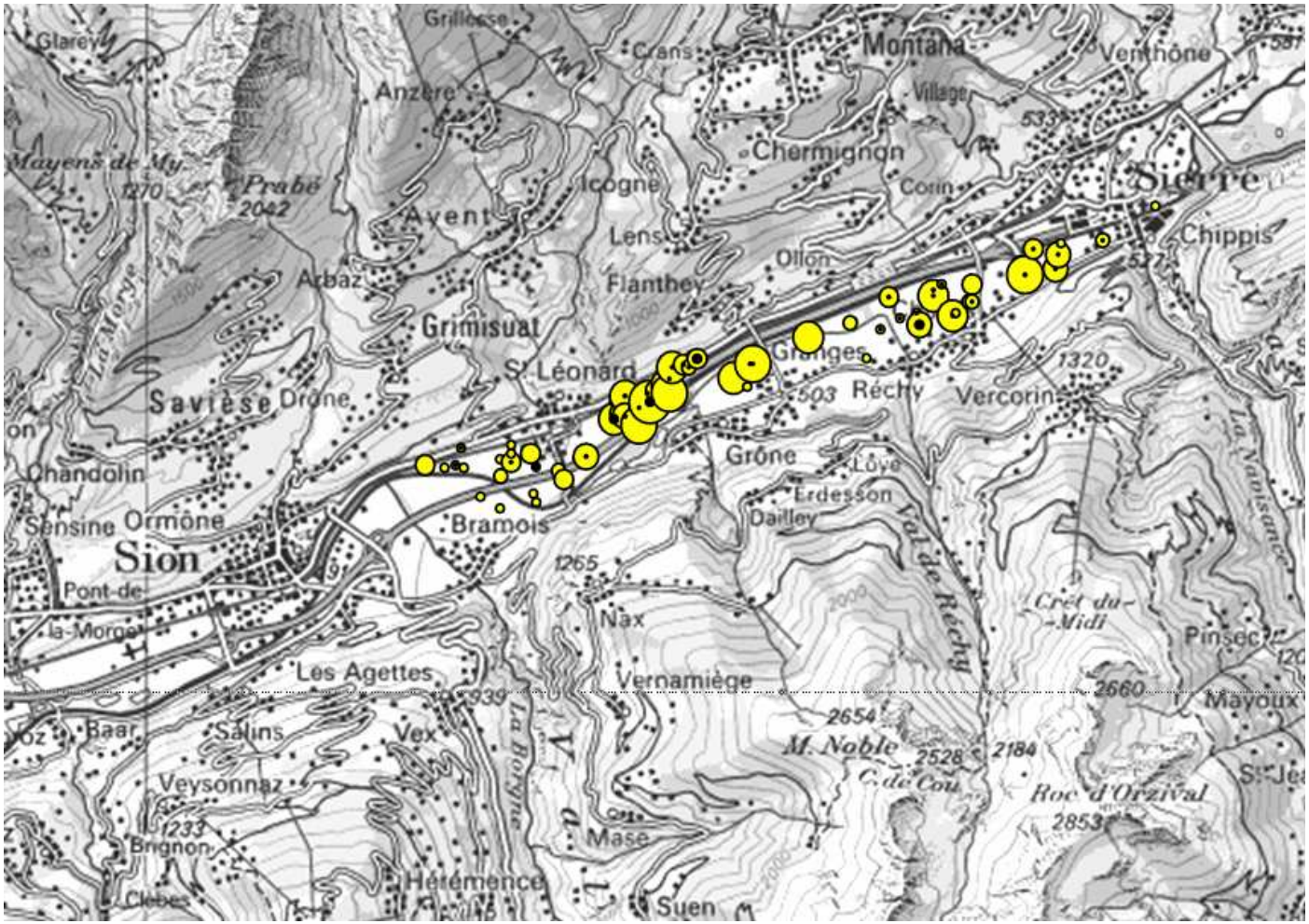

Glarey
Grillesse
Crans
Montana
Venthône
Anzère
Village
Mayens de My
1270
Prabé
2042
Chermignon
Icogne
Corin
Sierre
Avent
Lens
Chippis
Ollon
Arbaz
Flanthey
Chalais
Grimisuat
Granges
St-Léonard
1320
Réchy
Vercorin
Savièse
Drône
Grône
Löye
Chandolin
Erdesson
Sensine
Ormône
Dailley
Sion
1265
Pont-de-
la-Morge
Nax
Les Agettes
Vernamiège
Pinsec
Mayoux
Baar
Salins
Vex
2654
M. Noble
2528
2184
Veysonnaz
Roc d'Orzival
2853
Brignon
Mase
Hérémence
Suen
Clèbes

Appendix 6: Map showing locations of nest boxes used by breeding hoopoes. Yellow circles indicate breeding the total number of breeding attempts at a location from year 2000 to 2007. Black circles correspond to the number of breeding attempts in 2007. Circles are proportional in size to the number of breeding attempts per location (ranging from 1 to 13 attempts).

a)



b)


Glarey
Grillesse
Crans
Montana
Vermône
Anzère
Village
Mayens de My
1270
Prabé
2042
Chermignon
Icogne
Corin
Sierre
Avent
Lens
Chippis
Ollon
Arbaz
Flanthey
Grimisuat
Granges
St-Léonard
1320
Réchy
Vercorin
Savièse
Drône
503
Grône
Löye
Chandolin
Erdesson
Dailley
Sensine
Ormône
Bramois
Sion
1265
Pont-de-
la-Morge
Nax
Les Agettes
Vernamiège
Pinsec
Mayoux
939
2660
2654
Baar
Salins
Vex
M. Noble
2528
2184
Veysonnaz
Roc d'Orzival
2853
1233
Brignon
Mase
Hérémence
Clèbes
Suen