Ecological compensation areas as potential habitat for reptiles: A case study on hedges in the Canton Basel-Landschaft, Switzerland

Master Thesis
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Table of contents

Abstract

Reptile populations are declining worldwide. Habitat degradation due to agriculture is among the most serious threats that reptiles face. In agricultural landscapes reptiles depend on extensively used areas. In this master thesis I present a quantitative assessment of the occupancy rate of 89 hedges (registered and subsidized as ecological compensation areas) by reptiles in the Canton Basel-Landschaft, Switzerland. I also assessed which features of the hedges and which characteristics of the surrounding landscape (measured at three spatial scales) determine occupancy of hedges by reptiles.

A likelihood-based methodology developed by MacKenzie et al. (2002) and implemented in program PRESENCE v.2 was used for the statistical analysis. For the statistical analysis, I put the variables into five groups according to their characteristics and selected the best models according to the AIC. To receive the model which describes the data best, I combined the best models of different groups.

I found four reptile species on hedges, the lizards *Lacerta agilis*, *Anguis fragilis*, *Podarcis muralis* and the snake *Natrix natrix*. *Lacerta agilis* was the most abundant species (estimated occupancy rate was 10.3%). The group which described the data best was the group 'Political relevant' that included variables describing features of the focal hedges. I believed that such variables are most easy to alter by the governmental conservation office. However, addition of models from the group 'Landscape' led to a better description of the data. The model which described occupancy of hedges best included Euclidean distance to the nearest *L. agilis* population, presence of thatch, age of the hedge, forest area within a radius of 500 m around the hedge, length of first class roads within a radius of 500 m around the hedge and area of the buffer within a radius of 500 m around the hedge. Thus, occupancy of hedges is determined by both local and landscape factors. Euclidean distance to the nearest *L. agilis* population had a strong negative influence, whereas presence of thatch had a strong positive influence on the probability of occupancy of hedges by sand lizards. Management practices such as planting of hedges in Euclidean distances to the nearest *L. agilis* population smaller than 200 m and obligatory strips of thatch on the hedges are likely to be most effective in increasing the rate of hedges occupied by *Lacerta agilis*.

Zusammenfassung

Reptilienpopulationen sind weltweit rückläufig. Zu den grössten Bedrohungen zählt die Abnahme geeigneter Lebensräume durch die Landwirtschaft. In Landschaften mit intensiver Landwirtschaft sind Reptilien auf extensiv genutzte Flächen angewiesen. In dieser Masterarbeit untersuchte in quantitativ, welcher Anteil der als ökologische Ausgleichsflächen registrierten und subventionierten Hecken im Kanton Basel-Landschaft (Schweiz) von Reptilien genutzt wird. Dabei untersuche ich auch, welche Eigenschaften der Hecken und welche Charakteristika der die Hecken umgebenden Landschaft (gemessen auf drei verschiedenen räumlichen Skalen) die Nutzung einer Hecke durch Reptilien bestimmen.

Eine „likelihood“ basierte Methode, entwickelt von MacKenzie et al. (2002) und im Programm PRESENCE v.2 implementiert, wurde zur statistischen Analyse verwendet. Für die statistische Analyse wurden die erklärenden Variablen, gemäss ihrer Charakteristika, in fünf Gruppen eingeteilt und die besten Modelle mit Hilfe des AIC ausgewählt. Um dasjenige Modell zu erhalten, welches die Daten am besten beschreibt, wurden dann die besten Modelle verschiedener Gruppen kombiniert.

Ich fand vier Reptilienarten an Hecken, die Eidechsen *Lacerta agilis*, *Anguis fragilis*, *Podarcis muralis* und die Schlange *Natrix natrix*. *Lacerta agilis* war die am häufigsten gefundene Art (der geschätzte Anteil besetzter Hecken betrug 10.3%). Die Gruppe „Political relevant“ beschrieb die Daten am besten. Diese Gruppe beinhaltete Variablen von Eigenschaften der untersuchten Hecken. Ich betrachtete solche Variablen als am ehesten durch die kantonale Naturschutzfachstelle änderbar. Das Hinzufügen von Modellen aus der Gruppe „Landschaft“, führte jedoch zu einer besseren Beschreibung der Daten. Dasjenige Modell, welches schliesslich die Daten am besten beschrieb, beinhaltete die euklidische Distanz zur nächsten *L. agilis* Population, das Vorhandensein von Altgras, das Alter der Hecke, die Waldfläche in einem Radius von 500m um die Hecke, die Länge der 1.-Klasse-Strassen in einem Radius von 500m um die Hecke und die Fläche des Buffers in einem Radius von 500m um die Hecke. Ob eine Hecke besetzt ist wird also sowohl von lokalen Faktoren, als auch von Faktoren der Umgebung bestimmt. Die euklidische Distanz zur nächsten *L. agilis* Population hatte einen starken negativen Einfluss, das Vorhandensein von Altgras einen starken positiven Einfluss auf die Wahrscheinlichkeit der Besetzung der Hecken durch Zauneidechsen. Pflegemassnahmen wie das Anpflanzen von Hecken in euklidischen Distanzen weniger als 200m zur nächsten *L. agilis* Population, sowie die

Schaffung von Altgrasstreifen scheinen am effektivsten zu einer Erhöhung der Anzahl der von *Lacerta agilis* besetzten Hecken beizutragen.

Introduction

Reptiles face several threats that lead to declines of their population size. The declines of many reptile populations are similar to those experienced by amphibians in terms of taxonomic breadth, geographic scope and severity (Gibbons et al. 2000). Beebee (1992) argues that the average proportion of endangered and vulnerable reptile species in European countries (32%) is marginally higher than that of amphibians (27%) which suggests that reptile declines go well beyond the high published amphibian declines (Houlahan et al. 2000, Stuart et al. 2004). In Switzerland 79% of 19 native reptile taxa are on the red list (Monney, Meyer 2005). Two important causes that contribute to the declines are the degradation and loss of natural habitats (Fritz and Sowig 1988; Podloucky 1988; Gibbons et al. 2000). For example, agriculture in the Los Haitises region (Dominican Republic) is reported to have had a strong negative impact on lizard diversity with particularly low species richness in the most heavily or most recently disturbed habitats (Glor et al. 2001).

Intensification of agricultural practices resulted in increased use of fertilizers and application of machines, which in turn led to a loss of non-crop features (Stoate et al. 2001) and consequently suitable reptile habitat. However, in agricultural landscapes, reptiles strongly depend on extensively used areas (Blab 1991; Hofer, Monney, Dušej 2001, Monney, Meyer 2005). Once abundant, reptile species that thrived in traditionally managed agricultural landscapes, have to cope with the few remaining natural areas nowadays. Removal of extensively used potential habitat for wildlife began already decades ago. In the 1960s, hedgerow removal began on a large scale in England and Wales (Robinson 2002). For example in Wintersingen (Canton BL, Switzerland), due to amelioration between 1983 and 1994, hedges and shrubs were reduced by 13% (Tanner & Zoller 1996).

Ecological compensation areas (ECA) are extensively used areas in agricultural landscapes and serve to compensate for the loss of remnants of natural or anthropogenic habitat in agricultural landscapes. Therefore, ECA are expected to be valuable habitat for many plant and wildlife. Examples for ECA include extensively used grasslands, wildflower strips, orchards and hedges. It has been shown that on this set-aside areas species number and population densities of birds, insects, spiders and plants are higher than on nearby located control areas under conventional agriculture. Furthermore, it has been found a usually positive influence of size and age of ECA on these variables (Van Buskirk & Willi 2004). Results of an evaluation of biodiversity on ecological compensation areas (ECA) in Switzerland were presented in 2005. The evaluation was targeted at plants, birds, spiders, carabids, butterflies and grasshoppers (Herzog et al. 2005). Unfortunately, reptiles are generally not included in assessment of the conservation value of ecological compensation areas (e.g. Van Buskirk and Willi 2004; Knop et al. 2006; Kleijn et al. 2006).

Hedges often serve as ECA and are generally judged to have a positive influence on biodiversity. On 363 hedgerows 529 plant species (149 wood species) were reported. On 15% of the hedges few endangered species were found, and on further 20% potentially endangered species were found. In all of the three study areas, most optimal sites in terms of rarity and specificity of spider species were hedges. For carabids the diversity of specialized species on hedges was greater than compared to arable land. Bird species seen as hedgerow indicators (e.g. *Hippolais icterina, Sylvia communis*) profited by valuable hedges (Herzog et al. 2005). Reptiles are often found on hedges (Blanke 2004; Hofer 1998; Klewen 1988; Monney, Meyer 2005; Podloucky 1988), yet the value of ECA hedges as reptile habitat has not yet been assessed.

In addition to being core habitat, linear elements like hedges can have corridor functions. Even highly mobile animals like birds, use hedgerows for short and long-distance movements (Hinsley & Bellamy 2000). Hofer et al. (2001) mention the role of hedges for reptiles in serving as both habitat and corridor. Furthermore, Hallwyler (1985) argues that hedges serve as habitat for 9 reptile and amphibian species. Hedges therefore seem to be part of reptile habitats in agricultural landscapes. Despite of the relevance of reptile conservation and the reported benefits of ecological compensation areas to promote biodiversity, occupancy status of hedges by reptiles in the Canton Basel-Landschaft is not known. Nevertheless, the role of hedges could be important, either directly as habitat or indirectly as corridors respectively stepping stone habitats.

Study Area

I visited hedges registered and subsidized as ecological compensation areas (ECA) in the Canton Basel-Landschaft. The Canton Basel-Landschaft is located in the north-west of Switzerland. In the east and north-east it borders on the Canton Aargau and the river Rhein that represents the border to Germany. In the north it borders on the Canton Basel-Stadt, in the west on France and a part of the Canton Solothurn, and in the south on the Cantons Solothurn and Jura. Five geographic regions characterize the Canton: the Leimental, the valley of the river rhine, the Tafeljura, the Kettenjura and the Laufental. Altitude of the Canton ranges from 246 m to 1169 m above sea level, altitude of the visited hedges ranged from 300 m to 640 m above sea level. The Canton Basel-Landschaft is divided by the Canton Solothurn in two main parts, a western and an eastern part. At the connection of the two parts the city of Basel and its suburbs, as well in the western as in the eastern part, represent an area where only few hedges are located. Registered hedges are typically not placed in suburban but agricultural landscapes. Therefore, I restricted selection to the more open, agriculturally dominated regions of both parts.

Questions and Hypotheses

The aim was to answer three questions:

(i) Which reptile species occupy how many hedges in the Canton Basel-Landschaft?

(ii) How do local, metapopulation and landscape factors influence species specific occupancy (i.e. the percentage of occupied hedges)?

(iii) At what spatial scale are metapopulation and landscape factors most important? (metapopulation = connectivity respectively Euclidean distance)

I expected occupancy of hedges to be different for the three target species with lowest occupancy rate for *Podarcis muralis*. Further, I assumed that structural diversity (e.g. presence of woody debris, heaps of stones and thatch on the focal hedge) increases the probability of reptiles occupying a hedge. I assumed to find a positive correlation with hedge-age. I also assumed to find a positive correlation with area of the buffers which were cut by rivers and streams. The species specific maximum distance from a population to the nearest hedge at which a hedge can be colonized by reptiles remained to be found. Reptiles are generally poor dispersers. Therefore I expected metapopulation and landscape factors to be important at small scales.

Materials and Methods

Estimating occupancy: Data collection in the field

Baseline data on the distribution of reptiles and ecological compensation areas ('ECA', hedges and other types of set-aside) were taken from the reptile inventory of the Canton Basel-Landschaft, Switzerland (provided by Amt für Raumplanung, Abteilung Natur und Landschaft, Liestal, Switzerland), the GIS data base of the Landwirtschaftliches Zentrum Ebenrain (Sissach, Switzerland) and a digital map (1:25000, www.SWISSTOPO.ch). These three sources of information were combined using ArcExplorer (available for download at www.esri.com).

The most common reptile species *Anguis fragilis*, *Lacerta agilis* and *Podarcis muralis* were defined as target species (*Lacerta vivipara*, although common, was not expected to occupy hedges). Among the different types of ecological compensation areas, I selected hedges because they are commonly used by reptiles (Baur et al. 1997; Hofer, Monney, Dušej 2001).

To estimate occupancy of hedges by reptiles, I selected 89 out of 345 hedges that were registered and subsidized as ecological compensation areas. Selection was based on three criteria: (i) The hedges had to be placed in a distance <2 km from the next reptile population according to the reptile inventory BL. (ii) The hedges had to be placed in an area with relative high-hedge-density (i.e., ≥2 hedges in a distance <1 km from focal hedge). (iii) Every major geographic region of the canton had to be represented in the sample.

I put the hedges into groups with an average of seven hedges per group such that it was possible to visit one group per day with a bicycle. On the first visit I visited the groups in an arbitrary order to get used to the locations of the hedges. For the second visit I created a random sequence of the groups which I retained for the following visits.

Field work was carried out from late April 2005 until beginning of September 2005. I visited each hedge at least four times (two of them five times) on 53 days I expected reptiles to be active (i.e. no rainfall, forecasted temperature >15 °C). Three of the four visits were done in the morning between sunrise and midday. Each hedge was visited once in the afternoon between 3 p.m. and 6 p.m. Whenever possible I took care to do the four visits on each hedge at four different daytimes. Depending on the relative position of the sun to the hedge, I walked either along the sunny side and back or one time around.

A species was recorded as either found (1) or not found (0) at each visit. I noted environmental factors I believed had an influence on detectability of reptiles. The covariates for detection probability were date of the visit, wind, clouds (both estimated according to the Beaufort-scale), temperature 10 cm above ground, height (<60 cm/>60 cm) and cover (dense/open) of surrounding vegetation and rainfall on previous day (yes/no). I also collected data on environmental factors I believed to influence occupancy by reptiles like presence of heaps of stones, presence of woody debris, presence of thatch, slope (flat/inclined) and age (<6 years/>6 years, i.e., the minimum term) of the hedge (Table 1).

Estimating Occupancy: Data collection with a GIS

Additionally to the data collected in the field, landscape covariates were measured with a geographic information system. The goal was to obtain local and landscape variables that might explain hedge occupancy by reptiles. This work was carried out by Flavio Zanini (EPFL, Lausanne) during his civil service at the KARCH. Software used for GIS analysis was MapInfo, MapBasic and Idrisi32.

The goal of the GIS analysis was to obtain data on the hedge itself, reptile populations nearby and the surrounding landscape. The analysis was performed at three spatial scales.

As a first step, Flavio Zanini created buffers at three spatial scales (100, 500 and 1000 m) around each hedge. The buffers had roughly the same shape as the hedge they belonged to. Because I assumed that reptiles do not cross streams and rivers, buffers were cut by rivers and streams. This reduction of buffer area was done by cutting buffers when they overlapped a river (converted in surface using a buffer of 2 m) and then manually deleting the non accessible areas (after disaggregating all the objects). From these three buffers, several types of environmental factors were measured, such as number of reptile habitats and land use (Table 1). Objects for reptile layers, HEDGE_total, COMP_total, FOREST and ROAD were combined and disaggregated to obtain the effective number of patches. The measured variables included area and perimeter of the visited hedge, area of the buffer, area and perimeter of forest, area, perimeter and number of hedges and other ECA (e.g. 'wildflower strips', extensively used grasslands), area and numbers of reptile objects and length of roads (all classes combined). Area and perimeter (polygon was converted into polyline) and number were computed using a script (MapBasic) written specifically for these analyses. Forest and road data were extracted from the VC25 database, the vector format of the 1:25000 topographical maps of Switzerland. VC25 was provided by the Federal Office of Topography (SWISSTOPO).

Moreover, some nearest neighbour distance variables were computed: Euclidean distance to the nearest reptile object (using Idrisi software with 10 m resolution), Euclidean distance to the nearest reptile object but avoiding forest (using Idrisi, but with a friction map for dispersal analyses; the matrix had the value 1 and the FOR-

EST area the value -1) and a connectivity measure derived from metapopulation theory that assumes exponential relationship between distance *d* between patches and connectivity s_j (Hanski 1994).

$$s_j = \sum_{j \neq i} \exp(-d_{ij})$$

Table 1 List of variables I used in the analysis of site occupancy and detectability.

Variable	Description	Method	Unit
Site specific variables collected during field work			
hstone	Presence of heaps of stones	Field	present/absent
wood	Presence of woody debris	Field	present/absent
thatch	Presence of old grass	Field	present/absent
age	Age of the hedge	Field	<6 years/>6 years
slope	Inclination of the hedge	Field	flat/inclined
Sampling specific variables affecting detectability collected during field work			
date	Date of the visit	Field	
temp	Temperature 10 cm above ground	Field	°C
cloud	Amount of clouds	Field	Beaufort (1/8-8/8)
wind	Wind velocity	Field	Beaufort (0-5)
rain	Rainfall on previous day	Field	yes/no
height	Height of surrounding vegetation	Field	<60 cm/>60 cm
cover	Cover of surrounding vegetation	Field	dense/open
Site specific variables derived using GIS			
areavisitedhedge	Area of visited hedge	GIS	m^2
perimvisitedhedge	Perimeter of visited hedge	GIS	m
buffercut	Area of cut buffer	GIS	m^2
forest	Forest area	GIS	m^2
forested	Length of forest edge	GIS	m
hedge	Hedge area	GIS	m^2
hedgeed	Length of hedge edges	GIS	m
hedgen	Number of hedge patches	GIS	
comp	Area of ECA (*other* than hedges)	GIS	m^2
comped	Length of ECA edges (*other* than hedges)	GIS	m
compn	Number of ECA (*other* than hedges)	GIS	
La	Area of *Lacerta agilis* objects	GIS	m^2
lan	Number of *Lacerta agilis* objects	GIS	
road1class	Length of 1-Class roads	GIS	m
road2class	Length of 2-Class roads	GIS	m
road3class	Length of 3-Class roads	GIS	m
road4class	Length of 4-Class roads	GIS	m
NND variables			
eudistla	Euclidean distance to the nearest *Lacerta agilis* object	GIS	m
fordistla	Distance avoiding forest to the nearest *Lacerta agilis* object	GIS	m
sila	Connectivity (Hanski 1994) to site i from *Lacerta agilis* object	GIS	-

ECA: ecological compensation areas

Estimating occupancy: Statistical analysis

To estimate occupancy of hedges by reptiles I used a methodology developed by MacKenzie et al. (2002) and implemented in program PRESENCE v.2 (available for download at www.proteus.co.nz). This is a likelihood-based method to estimate the proportion of sites occupied by a species when detection probability is less than 1 (assuming that no sites are colonized or go extinct during the period when data are collected). Sites must be visited multiple times and the species is recorded found (1) or not found (0) at each visit. In this way one can write a detection history for each site. It is possible to formulate a probability for every 'detection history'. For example, the probability for site *i* with detection history 1010 is

$$\psi_i p_{i1}(1-p_{i2})p_{i3}(1-p_{i4}),$$

where ψ_i is the probability that the species is present at site *i* and p_{it} is the probability that the species will be detected at site *i* at time *t,* given presence. Assuming independence of the sites, the product of all terms, one for each site, constructed in this manner creates the model likelihood for the observed set of data, which can be maximized to obtain maximum likelihood estimates of the parameters (MacKenzie et al. 2002). If ψ_i and p_{it} are constant across all monitoring sites, the combined model likelihood can be written as

$$L(\psi,p)=\left[\psi^{n.}\prod_{t=1}^{T}p_t^{nt}(1-p_t)^{n.-nt}\right]\times\left[\psi\prod_{t=1}^{T}(1-p_t)+(1-\psi)\right]^{N-n.}$$

N is the total number of surveyed sites, *T* the number of distinct sampling occasions, *n* the number of sites where the species was detected at time *t*, *n.* the total number of sites where the species was detected at least once (MacKenzie et al. 2002). Standard deviation of ψ is estimated by a nonparametric bootstrap method (MacKenzie et al. 2002). Covariate information for ψ and *p* can be easily introduced using a logistic model (MacKenzie et al. 2002). Because ψ does not change over time during the sampling period (an assumption of the model), appropriate site covariates would be time constant and site specific, whereas covariates for detection probabilities could be time varying and site specific.

Site covariates I used in my analysis were (Table 1): presence of heaps of stones, presence of woody debris, presence of thatch, hedge-age, hedge-slope, area/perimeter of the visited hedge, area of the cut buffer (at the spatial scales 100/500/1000 m), area/perimeter of forest (100/500/1000 m), area/perimeter/number of hedges (100/500/1000 m), area/perimeter/number of other ecological compensation areas *other* than hedges (100/500/1000 m), area/number of reptile objects (100/500/1000 m), length of roads (all classes combined; 100/500/1000 m), Euclidean distance to nearest reptile object, Euclidean distance to nearest reptile object but avoiding forest and connectivity (Hanski 1994). Sampling covariates used for the analysis of detection probability were: date of the visit, wind, clouds, temperature, rainfall on previous day, height and cover.

The algorithm that is used by program PRESENCE to search for the maximum of the likelihood function works best if the values of the covariates are close to zero. Therefore all continuous variables were standardized. I used an information-theoretic model selection (Burnham & Anderson 2002) approach to determine which variables were necessary to explain whether a hedge was occupied by lizards. The different models were compared using the Akaike Information Criterion (AIC),

$$AIC = -2\log(L(\psi,p)) + 2K \,,$$

where L is the likelihood, ψ the proportion of sites occupied, p the detection probability and K the number of parameters estimated in the model (Burnham & Anderson 2002). Lower AIC values indicate that a model is better supported by the data than a model with higher AIC value. Furthermore, Akaike weights indicate the relative support of a model (Burnham & Anderson 2002):

$$w_i = \frac{\exp\left[-\left(\frac{\Delta AIC_i}{2}\right)\right]}{\sum \exp\left[-\left(\frac{\Delta AIC_i}{2}\right)\right]}$$

with

$$\Delta AIC_i = AIC_i - AIC_{\min}$$

AIC_{min} is the lowest AIC-value among the candidate models (i.e. the best model).

For model selection I chose the following approach:

1. To find the model that explains detection probability best, seven environmental factors were combined and ranked according to their AIC. The model for detection probability with the lowest AIC was included in every model computed in the following steps (2-5). I also used the variable 'cover' for detection probability as sampling specific variable that also includes information of hedge structure.

2. In the beginning I had a set of 56 variables. In the first step of the site occupancy modelling process, these variables were put into five groups according to their characteristics (Table 2).

Table 2 The variables were put into five groups according to their characteristics.

Group	Argument	Included variables
Hedges	To see whether area, perimeter or number of surrounding hedges explain site occupancy best.	hedge (100/500/1000) hedgeed (100/500/1000) hedgen (100/500/1000)
Other ecological compensation areas	To see whether area, perimeter or number of surrounding ecological compensation areas (o*ther* than hedges) explain site occupancy best.	comp (100/500/1000) comped (100/500/1000) compn (100/500/1000)
Landscape	To see whether the surrounding landscape, in terms of area of cut buffers, area and perimeter of forest or length of roads, explains site occupancy best.	buffercut (100/500/1000) forest (100/500/1000) forested (100/500/1000) road1class (100/500/1000) road2class (100/500/1000) road3class (100/500/1000) road4class (100/500/1000)
Reptile objects	To see whether area or number of surrounding reptile objects explain site occupancy best.	la (100/500/1000) lan (100/500/1000)

Table 2 continued

Political relevant	To see whether attributes of the *focal* hedge itself (which I believed to be most easy to alter by the governmental conservation office), in terms of area and perimeter, distance to the nearest *Lacerta agilis* population, presence of structural elements, age, inclination or the surrounding vegetation, explain site occupancy best.	areavisitedhedge perimvisitedhedge eudistla fordistla sila hstone wood thatch age slope height cover

3. In every group the best combinations of variables were selected. Selection was based on the convention that models up to a ΔAIC of 2 units explain the data equally well (Burnham and Anderson 2002). This led to 20 *single* models that best explained the data *within* their respective groups (Table 3).

Table 3 Models with lowest AIC-value (ΔAIC=2) of each group.

Model	Group
p(height) *ψ*(hedgeed500, hedgen500)	Hedge
p(height) *ψ*(hedgen1000)	Hedge
p(height) *ψ*(hedge500, hedgeed500, hedgen500)	Hedge
p(height) *ψ*(hedge500, hedgen500)	Hedge
p(height) *ψ*(comped1000)	Other ecol. comp. areas
p(height) *ψ*(comp1000)	Other ecol. comp. areas
p(height) *ψ*(compn1000)	Other ecol. comp. areas
p(height) *ψ*(comped1000, compn1000)	Other ecol. comp. areas
p(height) *ψ*(compn100)	Other ecol. comp. areas
p(height) *ψ*(comp1000, comped1000)	Other ecol. comp. areas
p(height) *ψ*(forest500, road1class500)	Landscape
p(height) *ψ*(forest500, road1class500, buffercut500)	Landscape
p(height) *ψ*(la100, lan100)	Reptile objects
p(height) *ψ*(la100)	Reptile objects
p(height) *ψ*(eudistla, thatch, age)	Political relevant
p(height) *ψ*(eudistla, thatch, age, wood)	Political relevant
p(height) *ψ*(eudistla, thatch, hstone)	Political relevant
p(height) *ψ*(eudistla, thatch, age, hstone)	Political relevant
p(height) *ψ*(eudistla, thatch, wood)	Political relevant
p(height) *ψ*(eudistla, thatch, wood, hstone)	Political relevant

4. 'Winners' from the within-group analysis were combined to 106 *combined* models (e.g. best hedge-model + best landscape-model). This step tested whether processes at different scales jointly explained hedge occupancy (e.g. both characteristics of the hedge and the surrounding landscape are important).

5. This set of 106 *combined* candidate models was analysed with PRESENCE and ranked according to the corresponding AIC, to receive the model that explains the data best (i.e. the most parsimonious model).

Results

Estimating occupancy: Data collection in the field

On 53 days I visited a mean of 7 hedges per day between 26 April and 9 September 2005. I spent on average 14 minutes at each hedge (total 78.24 h). Measured temperatures ranged from 7.6 °C to 28.5 °C. Heaps of stones were present on 27 hedges (30.3%), woody debris on 62 hedges (69.7%) and thatch on 58 hedges (65.2%). 38 hedges were inclined (42.7%) and 60 hedges were estimated older than 6 years (67.4%).

On the 89 visited hedges in the Canton Basel-Landschaft four reptile species were found:

1. *Lacerta agilis*, found on 9 hedges (10.1%)
2. *Anguis fragilis*, found on 4 hedges (4.5%)
3. *Podarcis muralis*, found on 2 hedges (2.2%)
4. *Natrix natrix*, found on 2 hedges (2.2%)

Among this four species only *Lacerta agilis* was found on a sufficient number of hedges to perform a statistical analysis (see Appendix).

Estimating occupancy: Statistical analysis

In the first step of model selection, I combined the sampling specific environmental factors to receive the model that explains detection probability best. The model which included the variable ‘height’, turned out to have the lowest AIC value (Table 4). Thus, I always added ‘height’ in the analysis of the site specific environmental factors.

Table 4 Ranking of models for detection probability with Akaike weights ≥0.05.

Model	AIC	ΔAIC	*w*
p(height)	108.87	0.00	0.10
p(temp)	108.97	0.10	0.09
p(height, temp)	109.21	0.34	0.08
p(height, rain)	109.68	0.81	0.07
p(cover)	110.02	1.15	0.06
p(height, date)	110.29	1.42	0.05
p(rain)	110.36	1.49	0.05
p(height, temp, rain)	110.39	1.52	0.05

ΔAIC is the difference between the model with the lowest AIC and the given model, *w* is the Akaike weight.

In the second step, I put the variables into five groups according to their characteristics. I created the group ‘Hedges’ to see whether area, perimeter and number of surrounding hedges explain occupancy of the focal hedge best. The analysis showed variables of hedges in the 500 m and 1000 m buffer but no variables of the 100 m buffer among the models with Akaike weight ≥0.05. The best model included the variables ‘height’, ‘hedgeed500’ and ‘hedgen500’ (Table 5).

Table 5 Ranking of models in the group ‘Hedges’ with Akaike weights ≥0.05.

Group	Model	AIC	ΔAIC	*w*
Hedges	*p*(height) ψ(hedgeed500, hedgen500)	106.24	0.00	0.28
	p(height) ψ(hedgen1000)	108.01	1.77	0.12
	p(height) ψ(hedge500, hedgeed500, hedgen500)	108.04	1.80	0.11
	p(height) ψ(hedge500, hedgen500)	108.12	1.88	0.11
	p(height) ψ(hedgen500)	108.66	2.42	0.08
	p(height) ψ(hedgeed1000, hedgen1000)	109.00	2.76	0.07
	p(height) ψ(hedge1000, hedgen1000)	109.07	2.83	0.07

ΔAIC is the difference between the model with the lowest AIC and the given model, *w* is the Akaike weight.

I created the group ‘Other ecological compensation areas’ to see whether area, perimeter and number of other types of set-aside areas explain site occupancy of the focal hedge best. The analysis showed variables of the 1000 m buffer being most frequent (five out of seven) among the models with Akaike weight ≥0.05. The best model included the variables ‘height’ and ‘comped1000’ (Table 6).

Table 6 Ranking of models in the group 'Other ecological compensation areas' with Akaike weights ≥0.05.

Group	Model	AIC	ΔAIC	*w*
Other ecological compensation areas	*p*(height) *ψ*(comped1000)	106.79	0.00	0.16
	p(height) *ψ*(comp1000)	107.73	0.94	0.10
	p(height) *ψ*(compn1000)	108.03	1.24	0.09
	p(height) *ψ*(comped1000, compn1000)	108.55	1.76	0.07
	p(height) *ψ*(compn100)	108.59	1.80	0.07
	p(height) *ψ*(comp1000, comped1000)	108.62	1.83	0.07
	p(height) *ψ*(comped500)	108.85	2.06	0.06

ΔAIC is the difference between the model with the lowest AIC and the given model, *w* is the Akaike weight.

I created the group 'Landscape' to see whether surrounding landscape, in terms of area of cut buffers, area and perimeter of forest or length of roads, explains occupancy of the focal hedge best. The analysis showed variables of the 500 m buffer being most frequent (four out of five) among the models with Akaike weights ≥0.05. The best model included the variables 'height', 'forest500' and 'road1class500' (Table 7).

Table 7 Ranking of models in the group 'Landscape' with Akaike weights ≥ 0.05.

Group	Model	AIC	ΔAIC	*w*
Landscape	*p*(height) *ψ*(forest500, road1class500)	99.40	0.00	0.27
	p(height) *ψ*(forest500, road1class500, buffercut500)	100.26	0.86	0.17
	p(height) *ψ*(forest1000, forested1000)	102.06	2.66	0.07
	p(height) *ψ*(forest500)	102.37	2.97	0.06
	p(height) *ψ*(forest500, buffercut500)	102.79	3.39	0.05

ΔAIC is the difference between the model with the lowest AIC and the given model, *w* is the Akaike weight.

I created the group 'Reptile objects' to see whether area or number of surrounding reptile objects explain occupancy of the focal hedge best. The analysis showed only variables of the 100 m buffer among the models with Akaike weights ≥0.05. The best model included the variables 'height', 'la100' and 'lan100' (Table 8).

Table 8 Ranking of models in the group 'Reptile objects' with Akaike weights ≥0.05.

Group	Model	AIC	ΔAIC	*w*
Reptile objects	*p*(height) *ψ*(la100, lan100)	94.78	0.00	0.46
	p(height) *ψ*(la100)	95.08	0.30	0.40

ΔAIC is the difference between the model with the lowest AIC and the given model, *w* is the Akaike weight.

I created the group 'Political relevant' to see whether attributes of the *focal* hedge itself (which I believed to be most easy to alter by the governmental conservation office), in terms of area and perimeter, distance to nearest *Lacerta agilis* population, presence of structural elements, age, inclination or the surrounding vegetation, explain occupancy best. The analysis showed variables 'eudistla' and 'thatch' to be present among all models with Akaike weight ≥0.05. The best model included the variables ‘height’, ‘eudistla’, ‘thatch’ and ‘age’ (Table 9).

Table 9 Ranking of models in the group ‘Political relevant’ with Akaike weights ≥0.05.

Group	Model	AIC	ΔAIC	*w*
Political relevant	*p*(height) *ψ*(eudistla, thatch, age)	80.00	0.00	0.20
	p(height) *ψ*(eudistla, thatch, age, wood)	80.65	0.65	0.14
	p(height) *ψ*(eudistla, thatch, hstone)	80.68	0.68	0.14
	p(height) *ψ*(eudistla, thatch, age, hstone)	81.30	1.30	0.10
	p(height) *ψ*(eudistla, thatch, wood)	81.56	1.56	0.09
	p(height) *ψ*(eudistla, thatch, hstone)	81.57	1.57	0.09
	p(height) *ψ*(eudistla, thatch, age, hstone, wood)	82.20	2.20	0.07
	p(height) *ψ*(eudistla, thatch)	82.22	2.22	0.07

ΔAIC is the difference between the model with the lowest AIC and the given model, *w* is the Akaike weight.

Within-group analysis revealed that variables describing attributes of the *focal* hedge itself (summarized in the group ‘Political relevant‘), explained the data best. The model with the lowest AIC value included the variables ‘eudistla’, ‘thatch’ and ‘age’. The model with the lowest AIC value of the second best group had a ΔAIC value of 14.78 (Table 10). Models with such large ΔAIC value can be considered as poor descriptions of the data.

Table 10 Order of groups and their respective models with lowest AIC-values.

Group	Model	AIC	ΔAIC
Political relevant	***p*(height) *ψ*(eudistla, thatch, age)**	**80.00**	0.00
Reptile objects	*p*(height) *ψ*(la100, lan100)	94.78	14.78
Landscape	*p*(height) *ψ*(forest500, road1class500)	99.40	19.40
Hedge	*p*(height) *ψ*(hedgeed500, hedgen500)	106.24	26.24
Other ecological compensation areas	*p*(height) *ψ*(comped1000)	106.79	26.79

ΔAIC is the difference between the model with the lowest AIC and the given model.

The analysis of the set of 106 *combined* candidate models with PRESENCE identified the models that explained occupancy of hedges best. All of the five models with an Akaike weight ≥0.05 included the variables ‘eudistla’, ‘thatch’, ‘age’, ‘forest500’ and ‘road1class500’. Two of them included the variable ‘buffercut500’. The variables ‘wood’, ‘comp1000’ and ‘compn100’ were each included in one model. The model that explained occupancy best included the variables ‘eudistla’, ‘thatch’, ‘age’, ‘forest500’, ‘road1class500’ and ‘buffercut500’ (Table 11).

Table 11 Model selection to determine which variables describe abundance of *Lacerta agilis* on hedges best. Ranking of models with Akaike weight ≥0.05 and included variables with respective values.

Model	Included variables	AIC	ΔAIC	*w*	*K*
1	***p*(height) *ψ*(eudistla, thatch, age, forest500, road1class500, buffercut500)**	**72.33**	0.00	**0.28**	**9**
2	*p*(height) *ψ*(eudistla, thatch, age, forest500, road1class500, buffercut500, wood)	74.33	2.00	0.10	10
3	*p*(height) *ψ*(eudistla, thatch, age, forest500, road1class500, comp1000)	74.40	2.07	0.10	9
4	*p*(height) *ψ*(eudistla, thatch, age, forest500, road1class500)	75.13	2.80	0.07	8
5	*p*(height) *ψ*(eudistla, thatch, age, forest500, road1class500, compn100)	75.55	3.22	0.06	9

ΔAIC is the difference between the model with the lowest AIC and the given model, *w* is the Akaike weight and *K* is the number of parameters used in the model.

Naïve estimate of hedges occupied by *Lacerta agilis* was 0.101. Proportion of occupied hedges as estimated with the best model by PRESENCE was 0.103 (SE 0.014). Thus, sand lizards were identified as present at all hedges where they occur. Average detection probability was 0.381 (Table 12).

Table 12 Proportion of occupied hedges and average detection probabilities of the best model.

Naïve estimate		0.101
Estimated proportion of occupied hedges		0.103
	SE	0.014
Average detection probability with the best model		0.381

Table 13 shows estimates and standard errors of explanatory variables included in the best models according to AIC with Akaike weight ≥0.05 (Table 11). A positive slope means that the variable influences site occupancy positively. In the model that explained occupancy of hedges best, forest area and the length of first class roads within the 500 m buffer and the area of the cut 500 m buffer had a moderate positive influence, presence of thatch had a strong positive influence; whereas hedge-age had a moderate negative influence and Euclidean distance to nearest *Lacerta agilis* population had a strong negative influence, i.e., hedges are more likely to be occupied by sand lizards if there is a sand lizard population nearby. The variable I used to model detection probability, height of surrounding vegetation, had a small positive influence, i.e. sand lizards are more easily found on hedges when surrounding vegetation height is below 60 cm.

Table 13 Slopes and standard errors (SE) of variables on the logit scale of the best models shown in table 11 with Akaike weight ≥0.05. Empty cells indicate that the variable is not included in the model.

Variable	Model	**1**	2	3	4	5
ψ						
Intercept	Slope	**-139.00**	-228.72	-73.94	-44.80	-41.59
	SE	**2.41**	1.95	6.92	4.54	5.02
eudistla	Slope	**-80.16**	-80.09	-42.48	-24.96	-23.04
	SE	**4.19**	4.40	-12.93	7.89	8.26
thatch	Slope	**88.59**	126.89	49.03	29.86	26.38
	SE	**3.05**	2.64	8.57	5.45	6.16
wood	Slope		51.45			
	SE		4.12			
age	Slope	**-16.95**	-16.93	-16.75	-7.12	-7.54
	SE	**4.49**	4.71	5.88	2.72	3.21
forest500	Slope	**7.20**	7.19	4.53	3.57	4.34
	SE	**3.35**	3.54	1.81	1.37	1.95
road1class500	Slope	**8.94**	8.93	6.64	2.95	4.23
	SE	**1.79**	1.86	2.25	1.35	2.07
buffercut500	Slope	**8.53**	8.52			
	SE	**2.86**	2.91			
comp1000	Slope			-8.67		
	SE			4.60		
compn100	Slope					1.57
	SE					1.47
p						
Intercept	Slope	**-0.96**	-0.96	-1.02	-1.00	-1.00
	SE	**0.53**	0.53	0.53	0.53	0.53
height	Slope	**1.00**	1.00	1.03	1.01	1.01
	SE	**0.72**	0.72	0.69	0.71	0.70

The probability that a hedge is occupied by *Lacerta agilis* went down markedly as Euclidean distance to the nearest *L. agilis* population increased. In fact data suggested probability to be close to zero at distances greater than 200 m (Figures 1- 5).

With greater area of the cut 500 m buffer the probability of occupancy decreased to a lesser extent as Euclidean distance to the nearest *L. agilis* population increased (Figure 1).

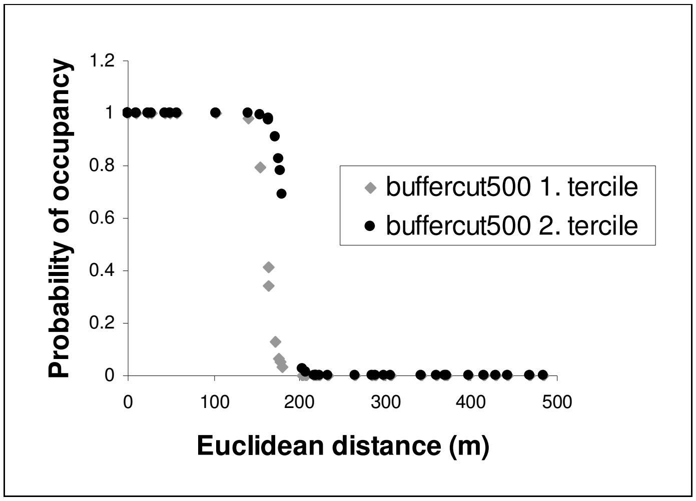

Figure 1 Probability of *Lacerta agilis* occupying a hedge as Euclidean distance to nearest *L. agilis* population increases on hedges with different level of area within the cut 500 m buffer (1. and 2. tercile). Probability of occupancy was 0 for all distances greater than 500 m.

With a greater amount of forest area within the 500 m buffer the probability of occupancy decreased to a lesser extent as Euclidean distance to the nearest *L. agilis* population increased (Figure 2).

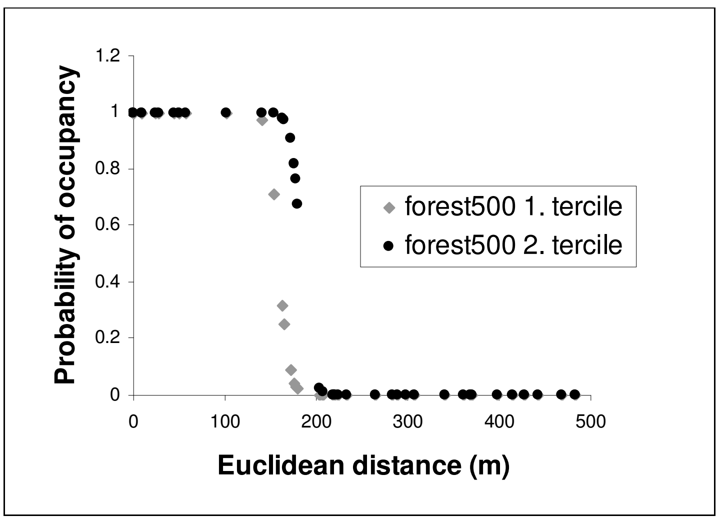

Figure 2 Probability of *Lacerta agilis* occupying a hedge as Euclidean distance to nearest *L. agilis* population increases on hedges with different amount of forest area within the 500 m buffer (1. and 2. tercile). Probability of occupancy was 0 for all distances greater than 500 m.

An increased length of first class roads within the 500 m buffer seemed to compensate for the distance effect (Figure 3).

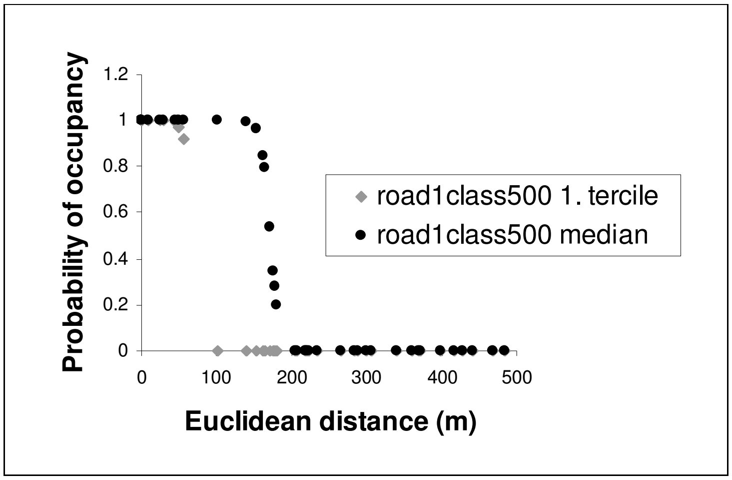

Figure 3 Probability of *Lacerta agilis* occupying a hedge as Euclidean distance to nearest *L. agilis* population increases on hedges with different amount of fist class roads within the 500 m buffer (1. tercile and median). Probability of occupancy was 0 for all distances greater than 500 m.

Data suggested probability of occupancy to remain higher on hedges estimated younger than 6 years compared to hedges estimated older than 6 years (Figure 4).

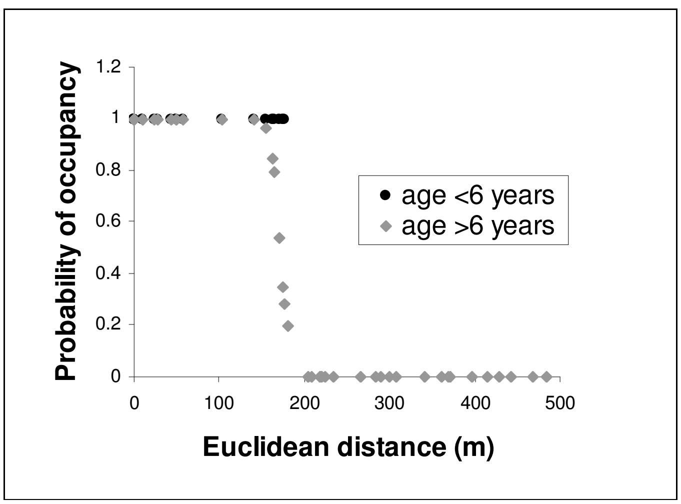

Figure 4 Probability of *Lacerta agilis* occupying a hedge as Euclidean distance to nearest *L. agilis* population increases on hedges that are estimated <6 y/>6 y. Probability of occupancy was 0 for all distances greater than 500 m.

Presence of thatch on hedges kept probability of occupancy high as distance increased up to 200 m to the nearest *L. agilis* population, whereas on hedges, where thatch was not present, probability was low even at small distances (Figure 5).

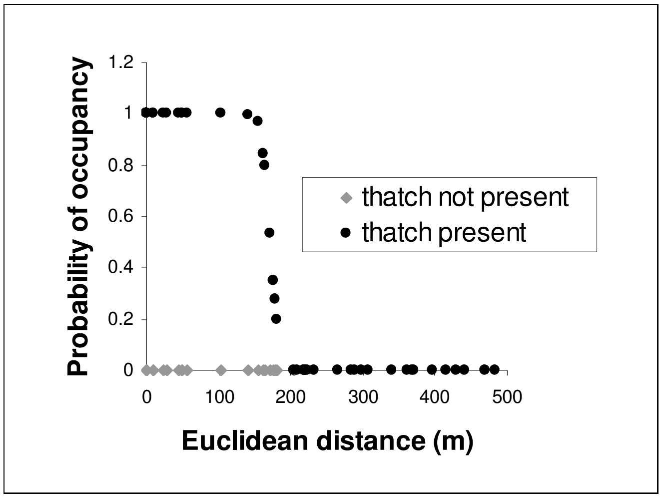

Figure 5 Probability of *Lacerta agilis* occupying a hedge as Euclidean distance to nearest *L. agilis* population increases on hedges where thatch is present/not present. Probability of occupancy was 0 for all distances greater than 500 m.

Finally, to evaluate management options, I calculated the 'suitability', i.e. probability of occupancy of all hedges in the data set using the values of the predictor variables. Additionally, I calculated the 'suitability' of the hedges under three management scenarios: i) assuming that the hedge was close to a source of colonists. To do so, I fixed Euclidian distance at 100 m, ii) assuming that 'thatch' was present on all hedges, and iii) a combination of i) and ii).

The distribution of occupation probabilities (ψ) of each of the 89 analyzed hedges with 'real' values for the environmental factors included in the best model (height, eudistla, thatch, age, forest500, road1class500, buffercut500) showed 78 hedges in the category 0-0.1, 7 hedges in the category 0.9-1 and 4 hedges in the categories between. If thatch was present, 68 hedges were in the category 0-0.1, 17 hedges were in the category 0.9-1 and 4 hedges were in the categories between (Figure 6).

However, if I kept all values but set Euclidean distance to nearest *Lacerta agilis* population to 100 m for each hedge, the distribution showed 47 hedges in the category 0-0.1, 38 hedges in the category 0.9-1 and 4 hedges in the categories between. If further, thatch was present, 32 hedges were in the category 0-0.1, 50 hedges were in the category 0.9-1 and 7 hedges were in the categories between (Figure 6).

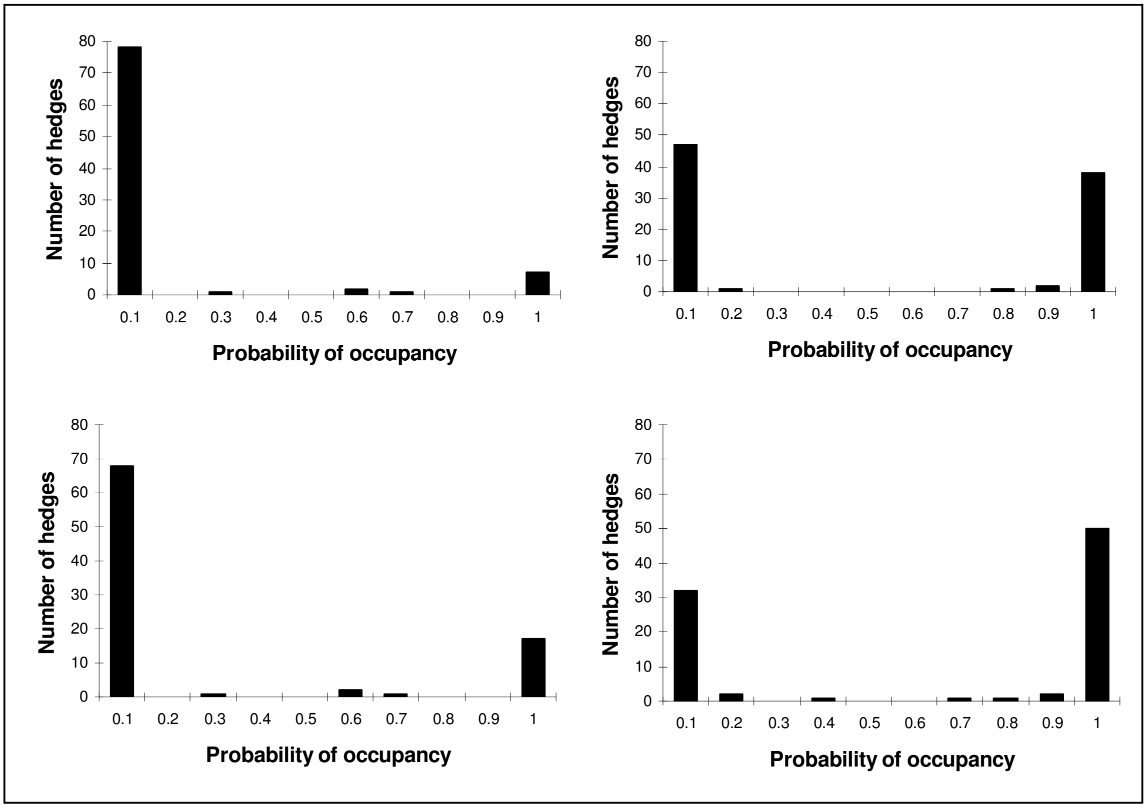

Figure 6 Distribution of occupation probabilities (ψ) of each of the 89 analyzed hedges under current conditions and given likely management options. Upper left figure: With 'real' values for the environmental factors included in the best model (height, eudistla, age, thatch, forest500, road1class500, buffercut500). Upper right panel: Predicted occupation probabilities with Euclidean distance fixed at 100 m. This scenario illustrates quality of hedges if they were planted close to existing sand lizard populations. Lower left panel: Predicted occupation probabilities if thatch would be present at all hedges. This scenario illustrates quality of hedges if farmers would leave a strip of thatch at each hedge. Lower right panel; Predicted occupation probabilities with Euclidian distance fixed at 100 m and thatch present. This scenario illustrates quality of hedges if they were planted close to existing sand lizard populations and if farmers would leave a strip of thatch at each hedge.

Discussion

Hedges often serve as ecological compensation areas (ECA) in agricultural landscapes. Even though reptiles are characteristic species of European agricultural landscapes and their survival depends on small structures such as ECA (Hofer, Monney, Dušej 2001), they have not been included in recent assessment of the use of ECA by wildlife and fauna (e.g. Van Buskirk and Willi 2004; Knop et al. 2006; Kleijn et al. 2006). This is the first study to quantify the use of ECA by reptiles.

Which reptile species occupy how many hedges?

The implicit question whether reptiles use hedges in the Canton Basel-Landschaft registered and subsidized as ECA can be answered affirmatively, which is rather not surprising. Reptiles use hedgerows as habitat and dispersal corridors (Hofer, Monney, Dušej 2001). Indeed, I found four out of seven reptile species, native to the Canton Basel-Landschaft, on hedges: *Lacerta agilis*, *Anguis fragilis*, *Podarcis muralis* and *Natrix natrix*. Looking at species specific occupancy, however, shows low rates for all species found.

Occupancy rates for *P. muralis* and *N. natrix*, both found on two hedges (2.2%), were expected to be low. I did not consider *N. natrix* as target species (as well as the other two native snake species *Coronella austriaca* and *Vipera aspis*). In general snakes are not as easy to find during surveys as lizards (Kéry 2002). One reason is that the time span during which snakes can be seen basking in the morning is relatively short. This would have reduced the number of hedges I could visit per day. Further, *N. natrix* is a highly mobile snake species whose preferred habitats are wetlands (Hofer, Monney, Dušej 2001). *N. natrix* is listed as endangered in the red list (Meyer, Monney 2005). Although I did not consider the grass snake as target species, the two findings support the role of hedges as habitat for snakes.

P. muralis, a species that prefers more vertical and stony habitats (Hofer, Monney, Dušej 2001), was considered as target species but I expected occupancy to be lower than for the other two species. More vertical and stony habitats are preferred as foraging and basking sites etc., however, nearby located hedges may be suitable egg laying sites by providing substrate.

A. fragilis is one of the most abundant and flexible reptile species in the Canton. In contrast to its high abundance and flexibility, I found only four hedges occupied (4.5%). I assume that the proportion of hedges occupied by *A. fragilis* is much higher. The main reason for non-detection is probably found in the survey method I used for all the three species. Slow worms spend a substantial amount of time underground and often hide under woody debris or stones. I detected four of the five individuals hidden under stones and only one individual on the bare ground. A survey method that consists of walking by watching out for reptiles (i.e., visual encounter survey), occasionally turning stones and woody debris seems therefore inadequate because the species is not available for detection most of the time. Alternatively I could have used corrugated iron sheets or wooden boards that serve as shelters and protected basking sites (as for example recommended in Common Standards Monitoring Guidance for Amphibians and Reptiles 2004). Such a method is applied successfully in snake monitoring. Since that would have meant a huge effort in terms of transporting the material and needed time to get permissions of all the owners of the hedges, I decided to do without.

I found 9 hedges to be occupied by *Lacerta agilis*. With occupancy of 10.1%, it was the most abundant reptile species I encountered on hedges. The statistical analysis with PRESENCE estimated the proportion of occupied hedges to be slightly higher (10.3%). This small difference between the naïve and the estimated occupancy indicates that I found all hedges occupied by sand lizards. Occupancy seems low for this species given that many authors mention it inhabits human influenced landscapes and structures including hedges (Klewen 1988; Podloucky 1988; Hofer 1998; Blanke 2004). Moreover, the sand lizard is listed as vulnerable in the national red list (Meyer, Monney 2005), and listed as endangered in the Canton Basel-Landschaft.

How do environmental factors influence species specific occupancy?

Within-group analysis revealed that variables describing attributes of the *focal* hedge itself (summarized in the group 'Political relevant'), explained the data best. The model with the lowest AIC value included the variables 'eudistla', 'thatch' and 'age' (Table 10). The model with the lowest AIC value of the second best group (Reptile objects) had such a great ΔAIC value that it can be seen as a poor description of the data (Table 10). Nevertheless, combining the best models of different groups (i.e., variables of the focal hedge + variables of the surrounding landscape), led to an even better description of the data (Table 11). Thus, whether a hedge is occupied depends both on local (hedge) and landscape factors. Still, this is a very desirable result, because it suggests that through appropriate management of hedges and through the establishment of new hedges close to existing reptile populations one can create new suitable habitat for sand lizards. Factors which act at larger spatial scales (such as the overall density of ECA) and which are harder to change through management practices are of relatively little importance. Thus, the variables I believe are most easily altered and implemented by the governmental conservation office, as well as accepted by farmers, also explain the data best.

Age of the hedge, presence of thatch and Euclidean distance to the nearest *L. agilis* population were the most important variables of the *focal* hedge in explaining hedge occupancy by sand lizards.

Age of the hedge had a strong negative influence (Table 13, Figure 4). In contrast to what I expected first, new hedges (<6 years) were more likely to be occupied by *L. agilis* than old (>6 years) hedges. On the one hand new hedges provide structurally less diverse vegetation, less understory vegetation and less shelter than old hedges. On the other hand new hedges provide more open vegetation (less shade), more vegetation-free spots and greater structural diversity in terms of heaps of stones and woody debris due to modern hedge management. This supports the view that the sand lizard prefers vegetation types in early successional stages with a dense but not fully closed understory (Podloucky 1988; Blanke 2004). However, preferred vegetation cover and height depends on the climatic region (Blanke 2004). Hofer et al. (2001) argue that sand lizards, like slow worms (*Anguis fragilis*) and common lizards (*Lacerta vivipara*), are tolerant of dense vegetation. If vegetation grows too dense and spots with bare soil become scarce, sand lizards may not persist in the long term because old hedges are too shady. Shade is a critical factor affecting the distribution of reptiles. For example, the overgrowing of suitable habitat by bushes and trees is seen as possible reason for local extinction of the Jura viper (*Vipera aspis*) in the northern Swiss Jura Mountains (Jäggi, Baur 1998). Periodic selective cuts to reduce shading are recommended for reptile targeted hedge management (KARCH 1997). In contrast to sand lizards, birds generally prefer taller hedges with a high density of mature trees (Fuller et al. 2001). Management practices promoting reptile diversity therefore may need to be balanced against practices that seek to enhance bird diversity (van den Berg et al. 2001).

Presence of thatch on the hedge had a strong positive influence (Table 13, Figure 5). This means the probability a hedge is occupied by *L. agilis* is higher on hedges where thatch is present. Grass that is not mowed dries and becomes felted. Such thatch offers dry basking sites and a refuge from predators (Blab 1991). Presence of thatch also turned out to play an important role in describing abundance of sand lizards on railway embankments (Graf 2005). Strips of thatch are stated among the recommended conservation measures for reptiles (Monney, Meyer 2005).

The distance to the nearest potential source had the strongest effect on occupancy of hedges. Euclidean distance to nearest *Lacerta agilis* object had a strong negative influence (Table 13, Figures 1-5). The probability of *L. agilis* occupying a hedge decreased sharply with increasing distance. At distances greater than 200 m the probability of *L. agilis* occupying a hedge was close to zero, suggesting that sand lizards in the Canton Basel-Landschaft do not successfully colonize empty habitat patches that are further away than Euclidean distances greater than 200 m from a source population. Although there exist reports of covered distances up to 4000 m (Klewen 1988), only few individuals of a population contribute to the colonization of new habitat patches (Blanke 2004). Additionally most individuals are relative stationary and juveniles are not targets of predation or territorial aggression from adults (Blanke 2004). It is remarkable that among the three distance measures (Euclidean, Euclidean but avoiding forest and connectivity after Hanski), the one turned out to be the best that included least assumptions about dispersal behaviour.

The amount of forest area, the area of the cut buffer and the length of first class roads were the most important landscape variables in explaining hedge occupancy by *Lacerta agilis*.

With greater area of the cut 500 m buffers the probability of occupancy decreased to a lesser extent as Euclidean distance to nearest *L. agilis* population increased (Table 13, Figure 1). Since the buffers were cut by rivers and streams, their area is an indirect measure of the amount of rivers and streams in the landscape surrounding the focal hedge. Sand lizards use a variety of habitats that also include river and stream banks and alluvial forests (Hofer, Monney, Dušej 2001; Blanke 2004). Therefore it is possible that some individuals cross the boundaries of the buffers by chance. Nevertheless, a greater amount of rivers and streams (i.e. a smaller area of the cut 500 m buffers) is likely to reduce the probability of immigration and consequently occupation of the focal hedges.

Forest area within the 500 m buffer around the hedge seems to have a moderate positive influence (Table 13, Figure 2). *Lacerta agilis* is a species that typically lives on the boundary between forest and open landscape, thus it is absent in closed forest but occurs on clearings, along forest roads and forest verges (Hofer, Monney, Dušej 2001; Blanke 2004). Within 500 m around hedges areas of closed natural forest are rare. Many forests show patterns of human influence like clear cuts, roads and sites for recreational activities.

The length of first class roads within the 500 m buffer around the hedge seems to have a moderate positive influence on hedge occupancy too (Table 13, Figure 3). Such an outcome may sound unusual at first, because roads are reported to have negative impacts on animal wildlife. Among those impacts are mortality from road construction, mortality due to collision with vehicles and modification of animal behaviour (Trombulak et al. 2000). Nevertheless, many reptile species live along roads and on road embankments. In the Canton Bern, Switzerland, the majority of *L. agilis* habitats are reported to be pioneer stands (38%), of which (24%) consist of road and railway embankments (Hofer 1998). Especially embankments of first class roads are managed regularly, which includes mowing of grass and cutting of fast growing shrubs. Due to this management practices, although carried out primarily for safety and aesthetical reasons, an open vegetation structure is maintained that promotes suitable conditions for reptiles. Moreover, the barrier function of roads for reptiles is based on traffic volume rather than in the roads themselves. Lizards seem to be less threatened by road-kills compared to amphibians or other reptiles like snakes and turtles (Dodd et al. 2003; Pinowski 2005). In fact lizards on principle do not hesitate to cross roads. In the case of sand lizards, road embankments can be seen as dispersal corridors and stepping stone habitats.

The set of models with Akaike weight >0.05 also included some models that included variables of ecological compensation areas (*other* than hedges), namely area of ECA within the cut 1000 m buffer and number of ECA within the 100 m buffer (Tables 11 and 13). However, the first appearing variable, 'comp1000', is included in a model with ΔAIC >2. Further, each of the two variables appeared only once. This suggests that other ECA have some small effect on hedge occupancy by sand lizards.

All three landscape variables included in the best model (Tables 11 and 13) are of medium spatial scale (500 m). Thus, characteristics of the landscape within 500 m around the hedges seem to explain the probability of occupancy much better than characteristics of small (100 m) or large (1000 m) scale. Interestingly, 500 meters is beyond the inferred threshold for dispersal of about 200 m.

Thus, determination of the suitability of hedges as habitats for *Lacerta agilis* depends *not only* on the hedges themselves, but on a combination of the focal hedge and the surrounding landscape. This result seems to support the need of information about ECA in the context of entire landscapes (Van Buskirk & Willi 2004).

***Propositions to increase occupancy of hedges by* Lacerta agilis**

As a final step of the analysis, I calculated some scenarios that may guide management of ECA hedges such that they may be (more) suitable habitat for sand lizards. To do so, I predicted the suitability of hedges assuming different management scenarios: 1) new hedges are planted close to existing source populations, 2) farmers leave a strip of thatch and 3) both 1) and 2) are implemented (Figure 6).

The calculation revealed that hedges fall into one of two clearly separated groups: hedges were either unlikely to be occupied (predicted occupancy <0.1) or suitable (predicted occupancy >0.9). Only few hedges were of medium suitability.

The fraction of suitable hedges slightly increased if thatch was present (scenario 2) and it increased to a greater extent if Euclidean distance was fixed at 100 m (scenario 1). The pattern of either high or low suitability with only few medium-suitability hedges still remained. Combining fixed Euclidean distance and obligatory presence of thatch led to the greatest amount of suitable hedges (scenario 3). In all management scenarios, however, there remained a large fraction of low-suitability hedges. Thus, only a subset of hedges can be managed in such a way that they become suitable for sand lizards. Because different animal groups require different types of hedges or hedges that are managed in a different way, one might only manage hedges that have a high predicted suitability in a reptile-friendly way. Hedges with a low predicted suitability, even when managed in a reptile-friendly way, could be managed in favor of other taxonomic groups.

Whenever possible, planning of new hedges should take the reptile inventory in account. It looks like in the Canton Basel-Landschaft, *Lacerta agilis* does not successfully colonize empty habitat patches that are further away than Euclidean distances greater than 200 m from a source population. Consequently, to facilitate colonization of suitable habitat, new hedges should be planted in a Euclidean distance less than 200 m to the next *L. agilis* population (see scenario 1, Figure 6).

Grass on hedges should only be mowed partially. Some strips of grass should be left standing (scenario 2, Figure 6). This leads to areas of dead, felted grass (thatch). Such thatch areas deliver basking sites and shelter.

First class roads are included in the best model, suggesting a moderate positive influence on occupancy of hedges. Through adequate management of road embankments, stepping stone habitats and dispersal corridors for reptiles can be created and maintained (Karch 1997). Grass on road embankments should be mowed every two to three years with thatch areas left. Shrubby vegetation should be cut back regularly in a way that not more than one quarter of the area is covered with shading woody vegetation (KARCH 1997).

Management of hedges is time consuming and requires a lot of knowledge of the plant species and wildlife. In Switzerland only 10% of the hedges are inscribed as ecological compensation areas (Herzog et al. 2005). While it looks like management of road embankments can be done in such a way that road embankments become suitable habitat for reptiles, hedge management seems not to utilize its full potential to promote reptiles. The role of hedges in promoting biodiversity depends on their management and structure (Ewald, Lobsiger 1997). Hedges may serve a valuable role in nature conservation through ECA, but this requires appropriate management targeted specifically towards species of conservation interest. Not only *Lacerta agilis* but also several other reptile species that occur on hedges, as for example *Anguis fragilis*, *Natrix natrix*, *Coronella austriaca* and *Vipera aspis*, are likely to benefit from such practices.

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Appendix

Presence (1) – absence (0) data at visits A - E of *Lacerta agilis*, *Anguis fragilis*, *Podarcis muralis* and *Natrix natrix* on the selected 89 hedges.

Hedge	Lacerta agilis					Anguis fragilis					Podarcis muralis					Natrix natrix				
ID	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
36	0	**1**	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
49a	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
49b	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
77	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
78	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
81a	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
81b	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
125	**1**	**1**	**1**	0	**1**	**1**	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0
155	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
173	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
246	**1**	**1**	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
248	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
251	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
321	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
337	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
404	0	0	0	0	-	0	0	0	0	-	0	0	0	**1**	-	0	0	0	0	-
421	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
431	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
473a	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
473b	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
474a	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
474b	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
474c	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
544	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
547	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
551	**1**	**1**	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
552	**1**	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
553	**1**	0	**1**	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
568	0	**1**	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
569	0	0	0	0	-	0	**1**	0	0	-	0	0	0	0	-	0	0	0	0	-
575a	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
575b	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
575c	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
626	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
627	0	0	0	**1**	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
628	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
629	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
648	0	0	0	0	-	**1**	0	0	0	-	0	0	0	0	-	0	0	0	0	-
795	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
806a	**1**	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
806b	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
844	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
846a	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
846b	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
848	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
857	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
939	0	0	0	0	-	0	0	0	**1**	-	0	0	0	0	-	0	0	0	0	-
953	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
956	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
957	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
964	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1014	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1049	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1234	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1245a	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1245b	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1348	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1398	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-

1399	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1486	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1487	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1498	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1499	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1500	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1508	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1558	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1560	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1562	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1570	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1689	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1691	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1692	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1696	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1697	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1773	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1828	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1833	0	0	0	0	-	0	0	0	0	-	0	0	**1**	0	-	0	0	0	0	-
1866a	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1866b	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1905	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1928	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	**1**	0	**1**	0	-
1930	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
1947	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
2028	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2033	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
2034	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
2108	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
2135	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-
2136	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-	0	0	0	0	-

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