Evidence-based evaluation of artificial reptile habitats:
A case study on stone structures

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Zusammenfassung

Das Problem des globalen Artensterbens stellt in der Naturschutzbiologie eine grosse Herausforderung dar. Ursache für das Aussterben einer Art ist oftmals Lebensraumverlust oder -fragmentierung durch menschliche Aktivitäten. Um diesem Artensterben entgegenwirken zu können, müssen Massnahmen eingeleitet, sowie Managementpläne konzipiert werden, mit dem Ziel, verbleibende Habitate zu schützen und aufzuwerten. Was dabei aber oft fehlt oder nur ungenügend durchgeführt wird, sind systematische Erfolgskontrollen der jeweils implementierten Pläne (Pullin and Knight 2001, Sutherland et al. 2004). Solche evidenzbasierten Evaluationen sind jedoch entscheidend, um erfolgreichen Natur- und Lebensraumschutz zu betreiben und tragen erheblich zur Verbesserung zukünftiger Projekte bei. Ein weiteres Problem in der Naturschutzbiologie ist, dass die Erhaltungs- und Managementpläne selten durch wissenschaftliche Erkenntnisse gestützt werden, sondern auf anekdotischen Quellen, persönlichen Erfahrungen und traditionellen Methoden beruhen (Pullin and Knight 2001, Sutherland et al. 2004). Der schlechte Zugang zu wissenschaftlicher Literatur sowie der grosse Zeitaufwand, diese oftmals englischsprachige Literatur zu lesen und zu interpretieren, sind für Naturschutzpraktiker Gründe, weshalb wissenschaftliche Informationen bei der Planung von Naturschutzstrategien nur unzureichend berücksichtigt werden (Pullin et al. 2004). Eine Datenbank, in welcher systematische Reviews über Erfolgskontrollen eingesetzter Erhaltungs- und Managementstrategien gesammelt und zusammengefasst werden und für Naturschutzpraktiker zugänglich sind, könnte die Lösung sein (Sutherland et al. 2004).

Diese Studie umfasst eine quantitative Evaluation einer in der Schweiz weit verbreiteten und empfohlenen Massnahme, sekundäre Reptilienhabitate aufzuwerten: der Bau von Steinstrukturen. Vor allem Bahnböschungen, welche oft extensiv genutzt werden, gute Verbreitungskorridore darstellen und somit im Reptilienschutz als Reptilienhabitate einen hohen Stellenwert besitzen, werden sehr oft mit Steinstrukturen versehen. Das Platzieren von Steinstrukturen wird als effektive Aufwertungsmassnahme angesehen, da sie die Strukturvielfalt entlang von Bahnböschungen erhöht. Reptilien brauchen gut strukturierte Habitate, denn als ektotherme Organismen müssen sie Ihre Körpertemperatur regulieren können, indem sie verschiedene Mikrohabitate nutzen (House et al. 1980, Edgar et al. 2010). Steinstrukturen stellen dabei nicht nur geeignete Sonnenplätze dar, sondern sie bieten auch Unterschlupf und dienen zum Teil sogar als Überwinterungsquartier. Die KARCH hat dabei detaillierte Anleitungen zusammengestellt, wie man geeignete Steinstrukturen baut (Meyer et

al. 2011). Obwohl diese Aufwertungsmethode mittlerweile in der Schweiz weit verbreitet ist, gibt es nur wenige Studien, welche die Effektivität dieser quantitativ untersucht haben.

Wir haben in dieser Studie das Vorkommen von Zauneidechsen *(Lacerta agilis)* und Mauereidechsen *(Podarcis muralis)* an 76 Steinstrukturen im Schweizer Mittelland untersucht. Die Verfügbarkeit von Daten aus 2007 (Reissner 2007, nicht publiziert) und neuen Daten aus 2013 haben es uns erlaubt, zu prüfen, ob sich am Vorkommen dieser zwei Arten an den Steinstrukturen in der Zwischenzeit etwas geändert hat. Mit Hilfe eines statistischen Modellierungsverfahren nach MacKenzie et al. (2003) und durch Miteinbeziehung von habitats-spezifischen Variablen (Appendix 1) wollten wir herausfinden, welche Variablen die Vorkommens-, Kolonisations- und Aussterbenswahrscheinlichkeit beeinflussen. Diese Parameter wurden unter Berücksichtigung der Antreffwahrscheinlichkeit geschätzt. Zusätzlich, mit Individuen-Zählungen aus 2013 und einem Modellierungsverfahren nach Royle (2004), wollten wir die Variablen, welche die Abundanz beeinflussen sollten, ausfindig machen. Die Abundanz wurde wiederum unter Berücksichtigung der Antreffwahrscheinlichkeit geschätzt.

Der Anteil besetzter Steinstrukturen hat sich für beide Arten zwischen 2007 und 2013 kaum geändert. Dies weist darauf hin, dass der Kolonisationsprozess der Steinstrukturen schon 2007 beendet war. Der geschätzte Anteil besetzter Steinstrukturen betrug sowohl im 2007 als auch im 2013 um die 30% für die Mauereidechse und 50% für die Zauneidechse.

In dieser Studie überschattete der Effekt der Konnektivität zu benachbarten Populationen den Effekt anderer Variablen auf die Vorkommenswahrscheinlichkeit und Abundanz. Für beide Arten stieg die Vorkommenswahrscheinlichkeit mit steigender Konnektivität rapide an (Figure 4A & 6). Unbesetzte Steinstrukturen wiesen für beide Arten einen durchschnittlich tieferen Konnektivitätswert auf als besetzte. Bei der Mauereidechse betrug der durchschnittliche Konnektivitätswert für unbesetzte Steinstrukturen sogar 0 (Appendix 6). Auch die Abundanz beider Arten stieg mit steigender Konnektivität an (Figure 8A & 10A). Eine erhöhte Konnektivität eines Habitats zu anderen Teilpopulationen ist insofern wichtig, da es die Wahrscheinlichkeit einer Re-Kolonisation im Falle eines Aussterbeereignisses erhöht (Hanski 1994, Haddad and Tewksbury 2006, Kindlmann and Burel 2008). Zudem haben eine erhöhte Konnektivität und somit eine erhöhte Frequenz an migrierenden Individuen einen positiven Effekt auf die Persistenz und Grösse einer Population (Haddad and Tewksbury 2006). Wenn Steinstrukturen also explizit dafür gebaut werden, um Populationen einer Zielart zu fördern, und wenn die Vorkommenswahrscheinlichkeit und Abundanz dieser Art maximiert werden soll, dann sollte man den ersten Fokus auf Böschungsabschnitte legen, welche eine hohe Konnektivität zu benachbarten Populationen dieser Art aufweisen. Die Konnektivität zwischen Populationen entlang von Böschungen kann zusätzlich durch eine extensive Nutzung dazwischenliegender Böschungsabschnitte maximiert werden.

Was Strukturmerkmale angeht, hatte die Länge und Höhe der Struktur einen positiven Einfluss auf die Abundanz der Mauereidechsen (Figure 10B), nicht aber auf die Abundanz von Zauneidechsen. Dahingegen bevorzugen Zauneidechsen moderat geneigte Böschungen (Figure 4B). Zudem fanden wir einen Effekt der Anwesenheit von Mauereidechsen auf die Abundanz von Zauneidechsen. Das beste Modell besagt, dass die Zahl an Zauneidechsen mit der Konnektivität steigt. Diese Zunahme wird stark unterdrückt, wenn Mauereidechsen vorhanden sind, als an Orten, wo nur Zauneidechsen vorkommen (Figure 8B). Tatsächlich wurden an Steinstrukturen, an denen beide Arten vorkommen, weniger Zauneidechsen beobachtet als an Steinstrukturen, an denen nur Zauneidechsen vorkommen. Dies weist auf eine Konkurrenzsituation hin, wobei es weitere Studien braucht, um das zu bestätigen bzw. zu widerlegen. Im Gegensatz zu den Mauereidechsen, welche in der Schweiz auf Expansionskurs sind, werden die Zauneidechsen als gefährdet eingestuft (Monney and Meyer 2005). Falls demnach eine solche Konkurrenzsituation bestätigt würde, sollten Böschungen so gestalten werden, dass besonders die Zauneidechse davon profitieren würde. Da die Zauneidechse zum Sonnenbaden eine Unterlage aus Holz bevorzugt (Blanke 2010), würde das platzieren von Holz- statt Steinstrukturen der Zauneidechse zu Gute kommen. Zudem sollte man nicht die Länge und Höhe einer Struktur maximieren, sondern deren Umfang. Zauneidechsen hielten sich bevorzugt in der Nähe der Vegetation auf, während Mauereidechsen meist über die ganze Struktur verteilt waren (persönliche Beobachtung). Letztendlich ist es durchaus denkbar, dass Zauneidechsen flache Steinlinsen und Steinhaufen bevorzugen, während die Mauereidechsen, mit ihrer hervorragenden Kletterfähigkeit, auch ganz gut mit Steinmauern zu Recht kommen.

Abstract

The global biodiversity loss has become a major challenge in conservation biology. To counteract these declines, the focus should be put on conserving and enhancing remaining habitats. Although many habitat management and conservation plans have been developed and implemented, insufficient attention has been given to evidence-based evaluations. However, quantitative evaluations of such plans are crucial to improve conservation action because of the limited amount of resources that is available for conservation. This study is intended to assess the benefits of a habitat management plan, which consists in enhancing artificial reptile habitats along railway embankments by placing stone structures. We applied a multi-season occupancy model proposed by MacKenzie et al. (2003) using detection/non-detection data collected over two years as well as a model to estimate abundance from repeated counts proposed by Royle (2004) using count data from 2013. The main goal was to detect changes in occupancy status and identify the site-specific environmental factors affecting occupancy rates, colonisation and extinction probabilities as well as abundance for two lizard species, the sand lizard (*Lacerta agilis*) and the wall lizard (*Podarcis muralis*). We also included observation covariates in order to account for imperfect detection. In this study, connectivity to neighbouring populations was by far the most important factor determining the occupancy and abundance of both species. Additionally, the inclination of the embankment affected the occupancy of sand lizards and the length and height of the structures influenced the abundance of wall lizards, indicating that habitat specific factors play a role, too. Our results also indicated a possible competitive situation between the two study species, as the abundance of sand lizards was lower when wall lizards were present. However, more studies are needed to confirm an effect of introduced wall lizards on the native sand lizard.

We believe stone structures to be an effective way to enhance artificial reptile habitats along railway embankments, as they were observed to be actively used by our study species. Stone structures provide structural variety and thus different microclimatic conditions, which are crucial for thermoregulatory behaviours of reptiles. Moreover, they can be used as stepping stones for dispersing individuals. Our results call for a combined approach where not only habitat suitability but also habitat connectivity are both enhanced all along railway embankments.

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1. Introduction

1.1. The importance of evidence-based conservation

Biodiversity is dramatically declining globally. Consequently, conservation actions such as habitat preservations and habitat restorations are increasing on a global scale in attempt to slow down or even stop declines. Developing a conservation strategy involves an initial site audit, a phase in which clear objectives are set, a planning phase and the implementation process (Edgar et al. 2010). However, one major problem in habitat conservation and management is that scientific evaluation of effectiveness is lacking for many actions (Pullin and Knight 2001, Sutherland et al. 2004). A possible reason for this could be the limited availability of financial resources, which are mainly used for the implementation of a plan, instead of quantitative evaluations thereof (Heer et al. 2013). Additionally, as reported by Braunisch et al (2012), Swiss practitioners still give greater importance to questions about politics and species ecology rather than to issues on how effectively carry out evaluations. These evidence based evaluations are however fundamental for future management plans, as, in order to attain successful conservation albeit the limited amount of resources, it is crucial for decision makers to know whether a conservation plan is effective or not (Pullin and Knight 2001, Sutherland et al. 2004). Omitting evidence based evaluations can result in applying management strategies which are falsely believed to be effective and which could potentially lead to devastating consequences (Sutherland et al. 2004). According to Pullin et al. (2004), decisions on conservation and management actions should ideally be made considering existing evidence on effectiveness provided by scientific evaluations. However, generally, evidence-based information is still playing a small role in planning conservation actions, while decision makers largely rely on anecdotal sources, personal experience as well as traditional practices (Pullin and Knight 2001, Sutherland et al. 2004). It has been shown that conservation management planers from the United Kingdom and Australia indeed strongly rely on experience-based sources rather than evidence-based information (Pullin and Knight 2005). Sutherland et al. (2004) also report a scarce use of scientific evidence-based literature by conservation practitioners. Pullin et al. 2004 argue that this could be due to primary scientific literature being too hard to access and too time consuming and difficult to read and interpret. The usage of a database containing systematic reviews on evidence-based evaluations as it is done in medical practice could be the solution (Sutherland et al. 2004).

1.2. Habitat loss and fragmentation – major threats to reptile populations

Reptiles are experiencing a global decline, which can be compared to that of amphibians in terms of severity. Gibbon et al. (2000) provide a perspective on this issue by describing numerous causes - including loss of suitable habitats, use of pesticides and herbicides, invasive species but also climate change. Reptiles play a key role as indicator species for environmental quality considering their sensitivity to environmental changes as well as their high demands on habitat quality (Monney and Meyer 2005). Due to their limited dispersal ability, reptiles cannot cross large distances to find new suitable habitat (Edgar et al. 2010). Thus, habitat change, loss and degradation represent the main threats to them and have become an important conservation issue (Berney 2001, Meyer et al. 2009, Edgar et al. 2010, Böhm et al. 2013). Before agricultural intensification in the first half of the 20th century, reptiles benefited from traditional farming and their by-products such as clearance cairns, dry walls, or hedges (Berney 2001), whereas in today's intensively used agricultural areas, it is almost impossible for reptiles to find suitable habitats and hence, reptile presence is often restricted to small areas of low intensity land use. Therefore, from a reptile conservation point of view, there is an increased need for action to protect remaining reptile habitats and improve their connectivity (Berney 2001) as the survival of fragmented populations strongly depends on the sufficient connection of habitat patches by dispersing individuals (Kindlmann and Burel 2008) and the availability of corridors for dispersal. Especially less managed railway embankments are often the only corridors left to connect reptile habitats in intensively used environments (Reissner 2007, unpublished) and represent key habitats for numerous reptile species. The conservation value of extensively managed railway embankments and roads should not be underestimated, as they represent important dispersal corridors and potential habitats for reptiles and amphibians but also for small mammals (Carthew et al. 2013).

1.3. The significance of artificial stone structures in reptile conservation

Reptiles are ectothermic and need a heterogeneous habitat that offers both basking as well as hiding places. They need to be able to switch between different microhabitats in order to maintain optimal body temperatures (House et al. 1980, Edgar et al. 2010). The range of resources and microhabitats for reptiles on railway embankments can be additionally increased by purposefully placing stone structures, which should fulfil the same purpose as clearance cairns in the cultural landscape and could also function as small scale habitats for other animals. These structures not only provide a place for sunbathing but also a hiding place as well as a potential hibernation place, and their production does not depend on big costs and effort. In Switzerland, the construction of stone structures along railway and road embankments has become a widespread and recommended reptile habitat enhancement strategy. Meyer et al. 2011, for example, provide a detailed guidance on where and how to build structures which are suitable for reptiles. However, in spite of the potential of stone structures as an easy way to enhance extensively used areas, there are surprisingly only a few studies providing evidence for their effectiveness.

1.4. Aim of the study

The main objective of this project was to assess the benefits of stone structures for reptile populations, focusing on sand lizards (*Lacerta agilis*) and wall lizards (*Podarcis muralis).* Here we apply a multi-season occupancy model proposed by MacKenzie et al. (2003) using previous detection/non-detection data from Reissner's study in 2007 and new data from 2013, in order to detect changes in occupancy status and identify the site-specific environmental factors affecting occupancy rates, colonization and extinction probabilities. Moreover, abundance is estimated using repeated counts from 2013 (Royle 2004) and the underlying factors are determined. This study is intended to promote evidence-based conservation and will help to evaluate the effectiveness of use of stone structures in reptile conservation and habitat management.

2. Methods

2.1. Study species

This study looked at the occurrence and abundance of two lizard species, the sand lizard (*Lacerta agilis*) and the wall lizard (*Podarcis muralis*) on stone structures. The sand lizard can occupy a variety of habitats, in particular areas of low intensity use, mining areas, forest edges, railway and road embankments as well as gardens (Berney 2001). As sand lizards have relatively limited home ranges, their ideal habitat offers many microhabitats such as basking places, shelters and breeding sites (Edgar et al. 2010). The fact that their populations are rather small and strongly fragmented justifies their consideration as *vulnerable* (Monney and Meyer 2005). In contrast to other native reptile species, the distribution range of the wall lizard is increasing in Switzerland (Meyer et al. 2009). The species is therefore placed in the category of *least concern* in the Red List (Monney and Meyer 2005). While wall lizards are ubiquitous in southern Switzerland, the occurrence of this species in northern Switzerland is more conditional on the presence of stone structures and a southern exposition of the site (Berney 2001, Meyer et al. 2009).

Figure 1 The upper pictures show a male wall lizard (left) and a male sand lizard (right). The lower ones show a female wall lizard (left) and a female sand lizard (right). During the breeding season, male sand lizards show a bright green colour which makes them clearly distinguishable from female sand lizards and wall lizards.

2.2. Study sites

Reissner (2007) surveyed reptiles at 80 stone structures at different sites in Switzerland during 2007. In this study, we resurveyed 76 of the same structures during 2013, using similar methods to produce the multi-season occupancy data required to estimate colonisation and extinction probabilities. The remaining 4 stone structures were either removed through construction work or not found. The stone structures to be surveyed were chosen according to their accessibility and recommendations given by the KARCH and SBB in 2007 (Reissner 2007, unpublished) and are distributed among 7 sites in Zurich, 3 sites in Bern and one each in Solothurn and Basle (Figure 2).

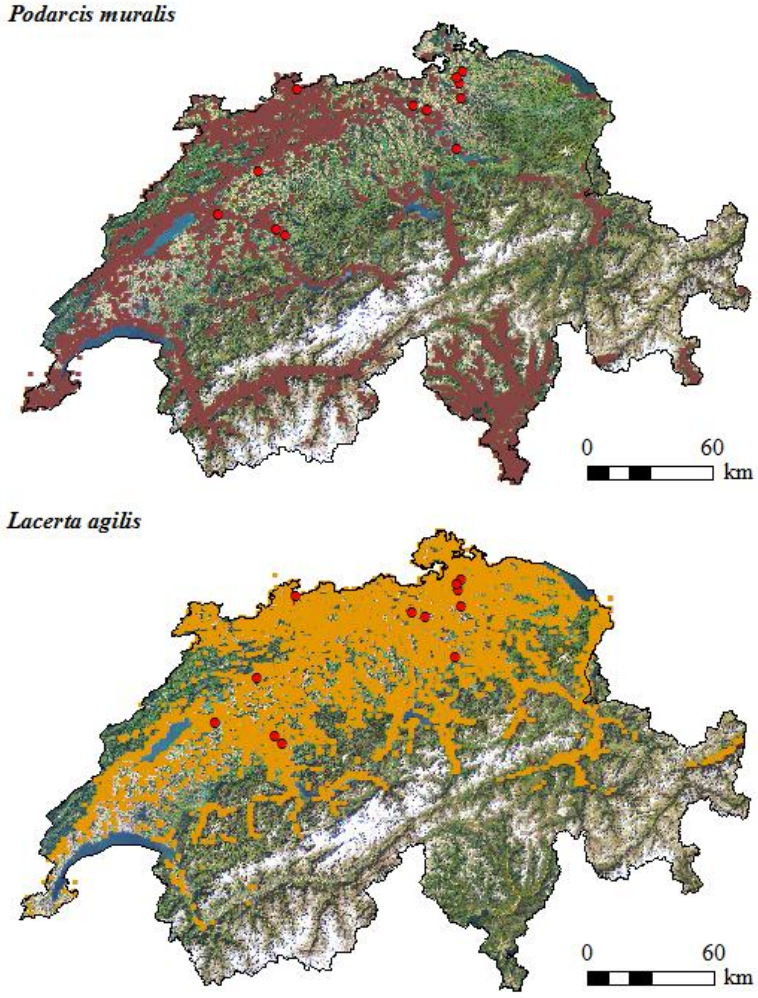

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Figure 2 The map on the top shows the distribution of the wall lizard in Switzerland, while the lower one shows the distribution of the sand lizard. The distribution data date back to 1975 and were provided by the CSCF. The red dots represent the study sites.

2.3. Data collection

From April to July 2013, we surveyed each structure at four sampling occasions and, if weather conditions allowed, at equal time intervals. Reissner (2007) surveyed each site nine times, so the dataset consists of 13 occasions over two years. In 2007, Reissner recorded detection and non-detection of the species as 1 and 0, respectively. In 2013, individuals were also counted during each site visit (and the count dichotomized to 0 and 1 for occupancy analysis). Fieldwork was carried out during sunny or cloudy days only, as lizards hide in their refuges during windy or rainy days. Since reptiles avoid excessive heat, we tried to carry out the summer surveys either in the morning or late afternoon. To meet the closure assumption (no changes in site occupancy state occur during the survey period; MacKenzie et al. 2002), intervals between sampling occasions were kept as short as possible.

At each stone structure, habitat variables which could explain abundance, occupancy, colonisation or extinction probabilities of lizards were recorded (Appendix 1). Measurements of covariates that reflect invariant features, such as structure length or embankment inclination, were taken from Reissner (2007). Covariates that potentially change between years, such as vegetation height, were measured in both 2007 and 2013. Additionally, repeatedly measured observation covariates were incorporated in the analysis to account for heterogeneous detectability and see which ones affect detection probability most.

2.4. Abundance, occupancy, colonisation and extinction variables

Habitat variables were chosen according to general recommendations on how and where to build a suitable stone structure (Meyer et al. 2011). Features like the length and height of a structure are used to determine whether the size of a stone structure influences occupancy or abundance of a species. Moreover, reptiles apparently prefer staying on the border regions where they can easily hide in the vegetation in case of danger. It is therefore suggested to maximize the circumference rather than area by constructing the stone structures in an irregular rather than uniform shape (Meyer et al. 2011). Thus, the shape of each stone structure was also recorded as irregular or uniform. Especially for sand lizards, sandy substrates are important for egg deposition (Edgar et al. 2010), hence, the presence of sand was also included in the analysis as a binary variable. Regarding the stone size, it is recommended to take various sized stones with diameters between 20 and 40 cm (Meyer et al. 2011). To test whether the stone size affects occupancy, colonisation or extinction, stone diameters were measured with a measuring tape and the mean value was considered for each structure. Stone sizes affect the spaces within the structure which gets more unsuitable for reptiles if the stones get too large or too small. Moreover, since it provides additional protection and hiding places, vegetation cover on the structure seem to be important as well, as long as it does not cover too much of it (Meyer et al. 2011). Vegetation cover was on one hand recorded as “present” or “absent”, on the other hand as the percentage of structure that was overgrown. The average vegetation height and density in a 3m radius around the structure was measured as well to test its influence on occupancy and eventually on colonisation and extinction probability. Too much shading through vegetation on and around the structure can lead to an insufficient heating up of the stones, which results in lizards leaving the structure and looking for a warmer basking place. Another explanatory variable, which we believe could be important for the abundance, occupancy, extinction and colonisation probabilities, is the age of the structure. Not accounting for other habitat variables, an older structure should theoretically have a higher probability to be occupied than a new one. Knowing the age of the structures in 2007, we could simply calculate the age of the same structures in 2013. The inclination of the embankment and hence of the structure was recorded in 2007 for all sites. Connectivity measurements were done partly in Quantum GIS 1.8.0. on available maps. Ideal reptile sites should contain multiple stone structures with a maximum distance of 20 to 30 meters between each other (Meyer et al. 2011) , so that, in case of an overcrowded or shaded structure, individuals can easily change to another one. We have calculated a connectivity measure using an equation from Hanski (1994) based on the Euclidean distance to neighbouring sites where populations of the target species have been observed (presence records of the two lizard species in the surroundings of the study sites was provided by the Swiss Biological Records Center CSCF). Finally, according to experts, a replacement of the sand lizard by the wall lizard is conceivable (Schulte et al. 2008). Thus, we included the presence of the other study species in the models to see whether it has an effect on the occupancy, abundance, colonisation and extinction probability of the target species.

2.5. Observation variables

Observation variables were chosen based on the knowledge of the natural history of the two lizard species. The date of the survey and the time of the day**,** at which the survey is performed are expected to affect detection probabilities in a non-linear way. Reptiles avoid excessive heat, thus, especially in mid-summer, it is recommended to carry out the surveys either in the morning or in the late afternoon, when solar radiation diminishes again. Cloud cover was estimated using an okta scale, a measure used in meteorology which describes how many eighth of the sky are covered by clouds. At warm, sunny days, cloud cover is expected to have a positive impact on reptile activity to a certain extent, since it reduces solar radiation as well. On the other hand, wind strength, which was measured on a Beaufort scale, is assumed to influence detection negatively. It agitates the surrounding vegetation and makes it more difficult for lizards to spot predators (Edgar et al. 2010). Additionally, wind chill cools down the body temperature, thus, at windy days, reptiles stay at more hidden places sheltered from the wind (Edgar et al. 2010). On rainy days, it is almost impossible to encounter reptiles but after a rainy period, we expect reptiles to be more detectable due to their increased necessity to hunt and bask (Niklaus Peyer, personal communication). Therefore, as another binary covariate, the rainfall in the previous 24 hours was also included in the analysis. Moreover, stone temperature might also have an influence on detectability and was measured at each stone structure using an infrared thermometer. Lizards are expected to bask preferably on stony surfaces since they warm up quickly and save the heat for a long period.

2.6. Statistical analysis

We z-standardized all continuous variables and checked for correlations between all explanatory variables of the data set. Data analysis was performed in R using the package *unmarked* (Fiske and Chandler 2011). We used multi-season site occupancy models to analyse the detection/non-detection data (MacKenzie et al. 2003). These models enable us to estimate initial occupancy (ψ_{07}), colonisation (γ) and extinction probability (ε) and detection probability (ρ) and to investigate potential effects of covariates on each of these parameters. We also used single season models by MacKenzie et al (2002) to analyse the data collected in 2013 and to estimate occupancy in 2013 (ψ_{13}).

To estimate the mean abundance (λ) in 2013 and find factors affecting it, an approach for spatially replicated counts (Royle 2004) was used. It should be noted that there is a difference between the detection probabilities estimated from the multi-season occupancy models and the one estimated from abundance models: Detection probabilities generated by using multi-season occupancy models represent the probability to detect at least one member of the population at a site, whereas detection probabilities estimated using abundance models are for individuals.

For both the occupancy and abundance modelling, we first fitted models for detection probability using candidate models (Table 1). To avoid overfitting, we decided to keep candidate models simple. Therefore, they contained one or two explanatory variables. We only used two explanatory variables in the same model when the correlation coefficient was smaller than r=0.3. The model best explaining detection probability was incorporated in further occupancy and abundance models and was used to generate abundance and occupancy estimates.

Table 1 Combinations of variables used to model detection probability for both sand lizards and wall lizards. These combinations were used to model detection probability in both the multi-season occupancy and abundance analysis.

	Model Covariates
1	cloud cover +cloud cover^2
2	visit duration
3	time of day +time of day^2
4	stone temperature +stone temperature^2
5	rainfall in previous 24h
6	date +date^2
7	wind strength
8	cloud cover +cloud cover^2 +visit duration
9	cloud cover +cloud cover^2 +time of day +time of day^2
10	cloud cover +cloud cover^2 +date +date^2
11	cloud cover +cloud cover^2 +stone temperature +stone temperature^2
12	cloud cover +cloud cover^2 +wind strength
13	visit duration +time of day +time of day^2
14	visit duration +stone temperature +stone temperature^2
15	visit duration +wind strength
16	time of day +time of day^2 +date +date^2
17	time of day +time of day^2 +stone temperature +stone temperature^2
18	time of day +time of day^2 +wind strength
19	date +date^2 + rainfall in previous 24h
20	stone temperature +stone temperature^2 +rainfall in previous 24 hours
21	stone temperature +stone temperature^2 +date +date^2
22	wind strength +date +date^2
23	wind strength +stone temperature +stone temperature^2

Burnham and Anderson (2001) stress the importance of making *a priori* considerations rather than using some type of data dredging. Thus, to model occupancy and abundance, we set up and tested a list of 28 *a priori* candidate models (Table 2) containing combinations of explanatory variables we expect to be biologically the most relevant among all the recorded variables. We then used AICc to rank models (Burnham and Anderson 2001). The top ranked model from our candidate model lists was considered to explain the data best. After ranking candidate models, we also used a stepwise approach to find the model best explaining the initial occupancy, colonisation and extinction probabilities as well as the abundance for both species. Stepwise model selection was based on AICc as well (Burnham and Anderson 2001). In both approaches, extinction and colonisation probabilities were not modelled using explanatory variables, as too few colonisation and extinction events were observed for both lizard species.

Table 2 *A priori* compositions of explanatory variables used to model the initial occupancy probability in 2007 as well as the abundance in 2013 for the two lizard species *Lacerta agilis* and *Podarcis muralis.*

	Model covariates
1	connectivity
2	age +age^2
3	presence of the other species
4	structure length +structure height +structure height^2
5	stone diameter +stone diameter^2
6	vegetation cover*
7	inclination +inclination^2
8	connectivity +age +age^2
9	connectivity +presence of the other species
10	connectivity +structure length +structure height +structure height^2
11	connectivity +stone diameter +stone diameter^2
12	connectivity + vegetation cover*
13	connectivity +inclination +inclination^2
14	age +age^2 +presence of the other species
15	age +age^2 +structure length +structure height +structure height^2
16	age +age^2 +stone diameter +stone diameter^2
17	age +age^2 +vegetation cover*
18	age +age^2 +inclination +inclination^2
19	presence of the other species +structure length +structure height +structure height^2
20	presence of the other species +stone diameter +stone diameter^2
21	presence of the other species +vegetation cover*
22	presence of the other species +inclination +inclination^2
23	structure length +structure height +structure height^2 +stone diameter +stone diameter^2
24	structure length +structure height +structure height^2 +vegetation cover*
25	structure length +structure height +structure height^2 +inclination +inclination^2
26	stone diameter +stone diameter^2 +vegetation cover*
27	stone diameter +stone diameter^2 +inclination +inclination^2
28	vegetation cover* + inclination +inclination^2

*For abundance analysis, we chose to include the amount of vegetation cover as explanatory variable in the candidate models. Since we do not have this information for 2007, we instead used the presence of vegetation cover as explanatory variable for initial occupancy.

3. Results

3.1. Multi-season occupancy models

3.1.1. *Lacerta agilis*

In 2007, sand lizards were observed at 35 of the 76 structures considered in this study, while 2013 they were observed at 26 structures. Colonisation events were observed at 11 of 76 stone structures between 2007 and 2013, while extinction events were observed at 20 structures.

The model best explaining the multi-season data for sand lizards accounted for 62% of the Akaike weight (Appendix 2). It included visit duration and the linear and quadratic effect of stone temperature as covariates for detection probability. In addition, initial occupancy was best explained by connectivity and the linear and quadratic effect of embankment inclination, the latter two having a non-significant effect (Table 3).

The mean detection probability was estimated at 20.97% (± 15.19%) and was highest at stone temperatures around 30° (Figure 3A). Furthermore, detection probability increased with the time spent at a site (Figure 3B).

Table 3 Beta estimates and p-values of explanatory variables contained in the top ranked *a priori* multi-season occupancy model for sand lizards. Since the data have been standardized, the estimates are directly comparable to each other.

Parameter	Explanatory variable	Estimate	Std. Error	p-value
initial occupancy	intercept	3.124	1.354	0.021
	connectivity	7.015	2.083	0.001
	inclination	-0.620	0.581	0.286
	inclination^2	0.557	0.548	0.309
colonisation probability	intercept	-10.200	38.800	0.793
extinction probability	intercept	-0.750	0.436	0.086
detection probability	intercept	-1.254	0.141	<0.001
	stone temperature	1.003	0.186	<0.001
	stone temperature^2	-0.416	0.115	<0.001
	visit duration	0.602	0.114	<0.001

The best model estimated colonisation probability to be close to zero while there was a substantial extinction probability ($\hat{\gamma}$ =0.00004 ±0.0015, $\hat{\varepsilon}$ =0.32 ±0.1). Extinction and colonisation probabilities were not modelled using covariates, since any covariate added led to huge standard errors. Thus, we decided to keep the “null” model only including the intercept for these two parameters (Table 3). The estimated occupancies obtained by using the best model only correcting for imperfect detection, were higher than the observed occupancy in both years ($\widehat{\psi}_{07}$=0.59 ±0.08, $\widehat{\psi}_{13}$=0.54 ±0.09). Initial occupancy was significantly affected by connectivity (Figure 4A), while both the linear and quadratic effects of inclination were not significant and showed high standard errors.

When removing either the quadratic or the linear effect of inclination from the top model, the AICc value only changed little (Appendix 3), indicating a weak effect of inclination on initial occupancy. On the other hand, when removing connectivity, the AICc increases by 23.9 supporting its inclusion and underlining the importance of this explanatory variable for initial occupancy.

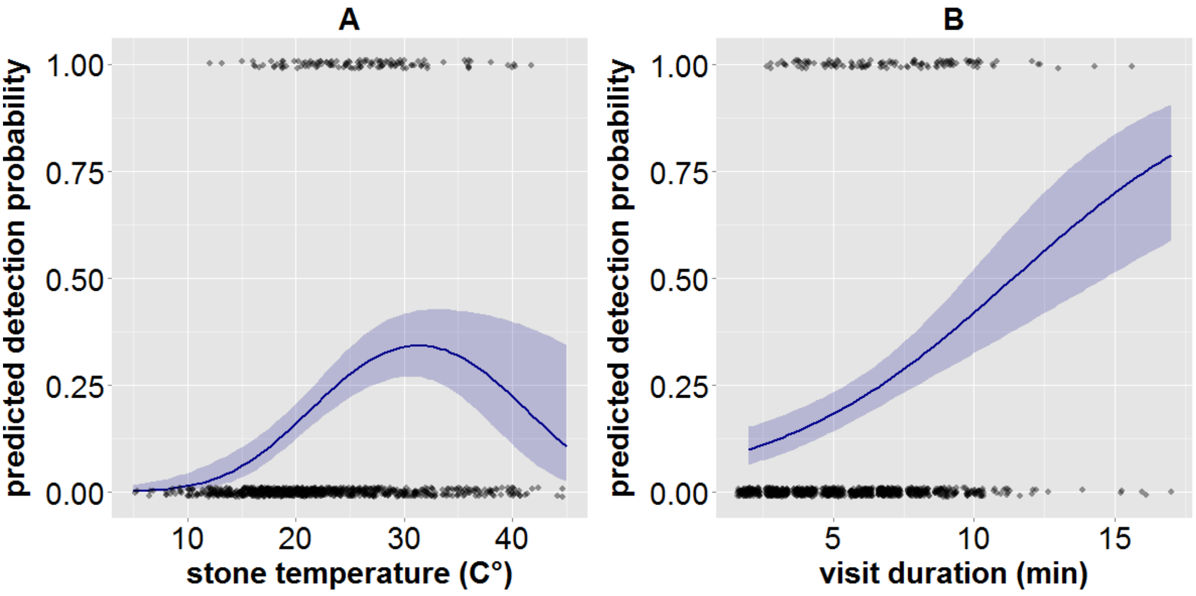

Figure 3 The effect of stone temperature (A) and visit duration (B) on the probability of detecting sand lizards predicted by the best occupancy model (blue line). The blue area represents the 95% confidence interval. Detection/non-detection data for each structure and each occasion is plotted as black dots.

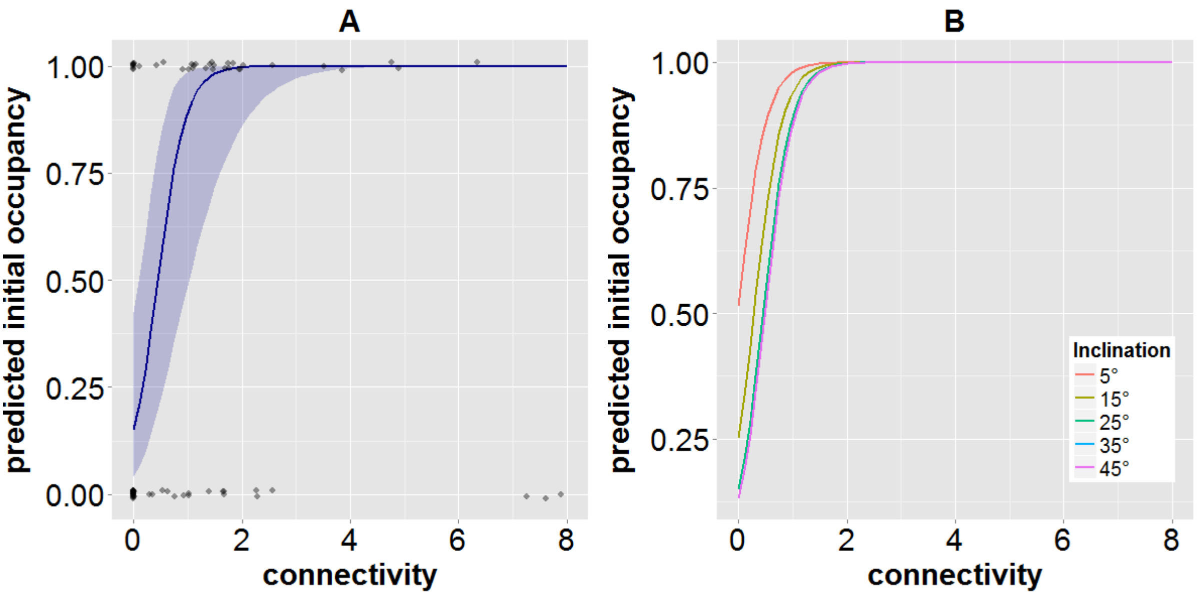

Figure 4 The effect of connectivity on initial occupancy for sand lizards predicted by the best occupancy model for the sand lizard (A). Plot B shows how predicted occupancy changes with connectivity at different embankment inclinations. The dots in plot A represent the sites at which sand lizards were observed at least once (1) or not observed at all (0).

3.1.2. *Podarcis muralis*

Wall lizards were detected at 25 of 76 structures considered for this study in 2007 and at 22 structures in 2013. There were no observed colonisation events between 2007 and 2013 and only 3 observed extinction events for the wall lizard.

The top ranked multi-seasonal model for wall lizards showed an Akaike weight of 57.1% (Appendix 2) and contained stone temperature and cloud cover as covariates for detection probability as well as connectivity being the only explanatory variable for initial occupancy, although its effect was not significant (Table 4).

The mean detection probability was estimated at 44.5% (± 22.58%). It is highest at stone temperatures around 30° (Figure 5A), where the model predicts a detection probability of about 80%, and decreases with cloud cover (Figure 5B).

Both colonisation and extinction probability estimates are close to zero ($\hat{\gamma}$=0.000008 ±0.0403, $\hat{\varepsilon}$=0.00012 ±0.0038), thus it is likely that neither colonisation nor extinction events have occurred. As almost no extinction events and no colonisation events were observed and the estimated values thereof were extremely low, it would not make sense to model extinction and a colonisation probabilities using covariates.

Table 4 Beta estimates and p-values of explanatory variables contained in the top ranked *a priori* occupancy candidate model for wall lizards. Since the data have been standardized, the estimates are directly comparable to each other.

Parameter	Explanatory variable	Estimate	Std. Error	p-value
initial occupancy	intercept	4.480	10.800	0.678
	connectivity	22.400	28.700	0.436
colonisation probability	intercept	-11.700	49.400	0.813
extinction probability	intercept	-9.060	32.300	0.779
detection probability	intercept	0.683	0.278	0.014
	stone temperature	1.311	0.210	<0.001
	stone temperature^2	-0.664	0.150	<0.001
	cloud cover	-0.395	0.155	0.011
	cloud cover^2	-0.429	0.226	0.058

Thus, as it is also the case for the sand lizard, we kept the "null" model for these two parameters (Table 4). The estimated occupancies obtained by using the best model for detection probability were equal to the observed occupancy in 2007 and slightly higher in 2013 ($\widehat{\psi}_{07}$=0.33 ±0.05, $\widehat{\psi}_{13}$=0.35 ±0.07). The variable best explaining wall lizard occupancy in 2007 was connectivity (Figure 6), whereby there are high uncertainties regarding its effect considering the high estimate values and the even higher standard errors (Table 4).

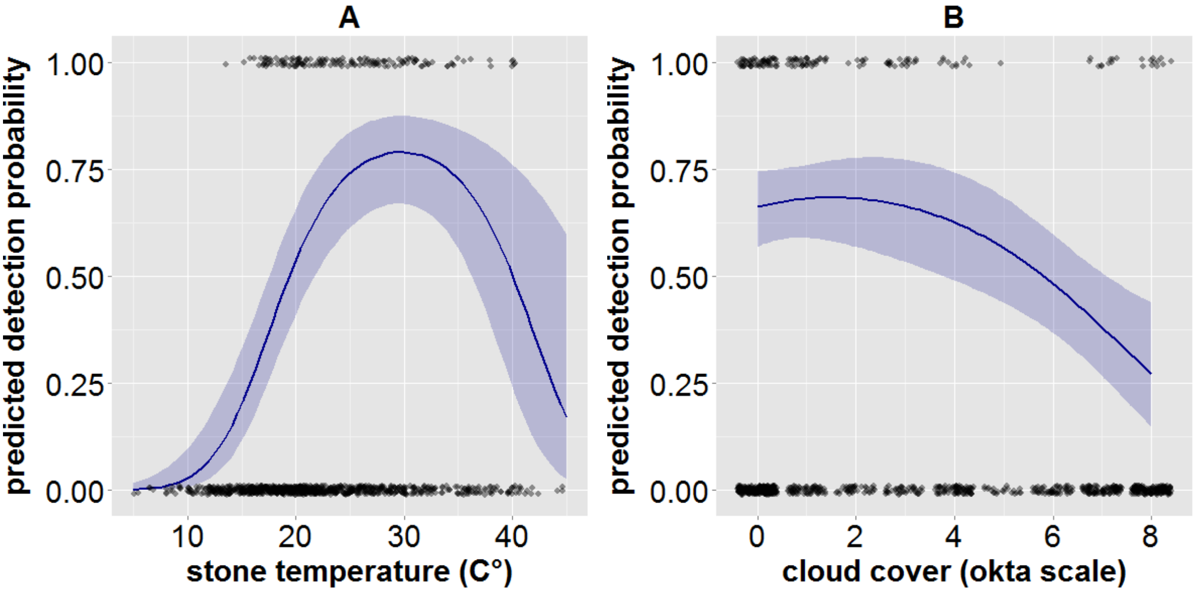

Figure 5 The effect of stone temperature (A) and cloud cover (B) on the detectability of wall lizards predicted by the best occupancy model (blue line). The blue area represents the 95% confidence interval. Detection/non-detection data for each structure and each occasion is plotted as black dots.

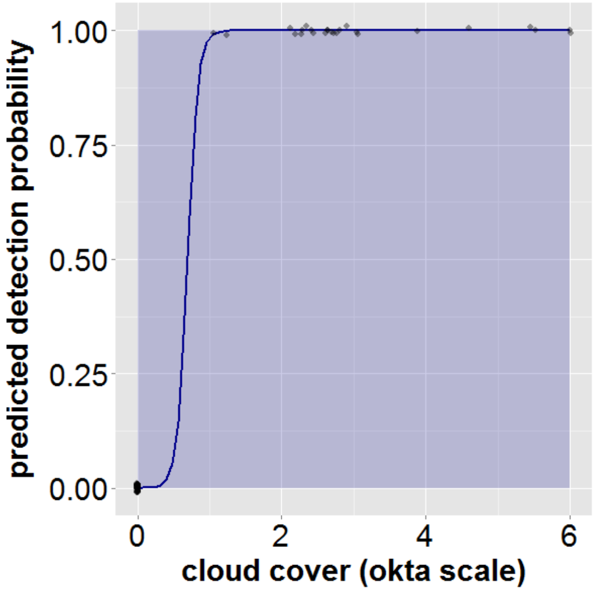

Figure 6 The effect of connectivity on initial occupancy for wall lizards according to the best occupancy model (blue line). The blue area represents the 95% confidence interval. The dots represent the sites at which sand lizards were detected at least once (1) or not detected at all (0).

3.2. Abundance models

3.2.1. *Lacerta agilis*

The best model explaining sand lizard abundance shows an Akaike weight of 82.9% (Appendix 4). It includes the linear effect of visit duration and the linear and quadratic effect of the time of the day as variables explaining detection probability, as well as connectivity and the presence of wall lizards as variables affecting abundance, the latter having a negative effect (Table 5). The probability to detect one individual of the sand lizards was again positively affected by the visit duration (Figure 7B) and changed among daytimes (Figure 7A).

Table 5 Beta estimates and p-values of explanatory variables included in the best *a priori* candidate abundance model for the sand lizard. Since the data have been standardized, the estimates are directly comparable to each other.

Parameter	Explanatory variable	Estimate	Std. Error	p-value
abundance	intercept	0.939	0.287	0.001
	connectivity	0.838	0.147	<0.001
	presence of wall lizards	-3.041	0.629	<0.001
detection probability	intercept	-1.356	0.414	0.001
	visit duration	-0.423	0.161	0.008
	time of day	0.081	0.193	0.674
	time of day^2	-0.589	0.200	0.003

The number of sand lizards observed at one structure during 2013 ranged from 0 to 8 individuals. The mean abundance estimated by using the best model accounting for detection probability was $\hat{\lambda}$=1.77 (±0.42) individuals per site. Sand lizard abundance was positively affected by the connectivity of the site (Figure 8A) and strongly negatively affected by the presence of wall lizards (Figure 8B). Abundance of sand lizards is predicted to strongly rise with increasing connectivity of the site when there is no presence of wall lizards. On the other hand, when there are wall lizards, sand lizard abundance stay low.

When removing connectivity or presence of wall lizard from the best model, the AICc increases drastically, indicating a strong predictive power of the two variables (Appendix 5).

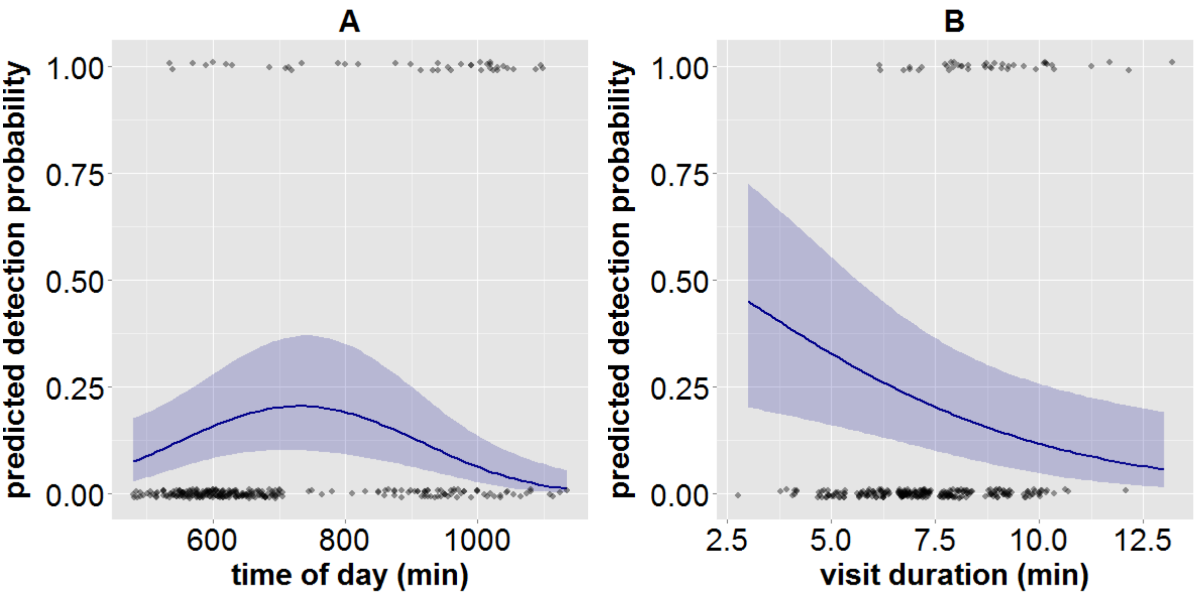

Figure 7 The probability to detect an individual of the sand lizards, predicted by the best abundance model (blue line), is affected by the time of day at which the survey is performed (A) as well as by the visit duration (B). The blue area represents the 95% confidence intervals. Detection/non-detection data for each structure and each occasion is plotted as dots.

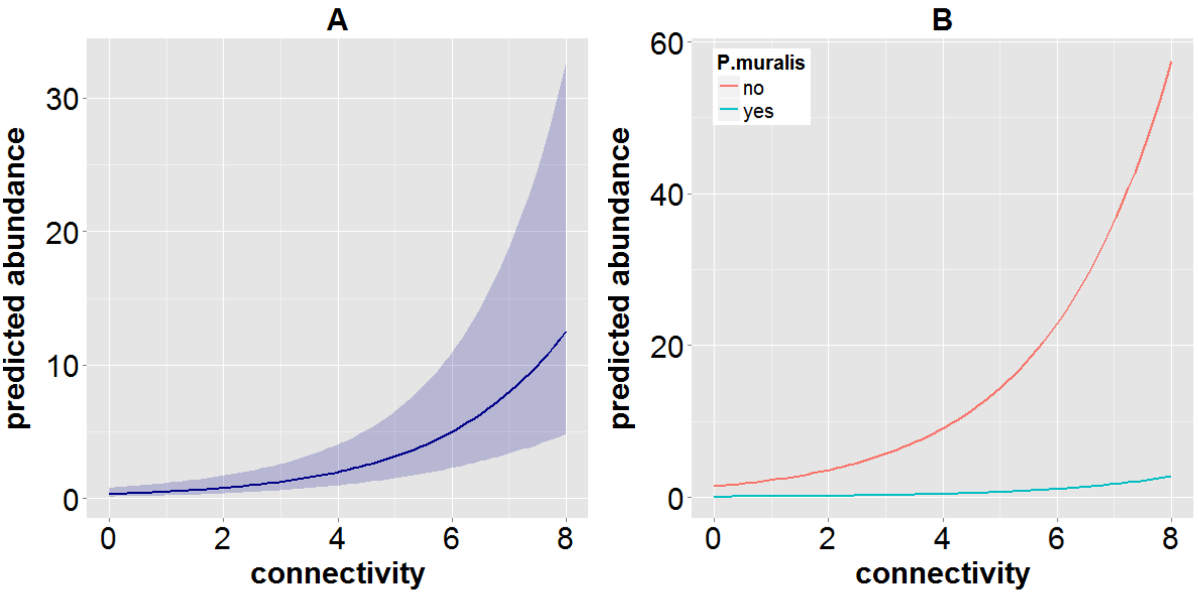

Figure 8 The effect of connectivity on the abundance of sand lizards predicted by the best abundance model (A). Plot B shows the difference in the effect of connectivity on abundance when only sand lizards occur (red line) or when sand lizards and wall lizards co-occur (blue line).

3.2.2. *Podarcis muralis*

The abundance data for wall lizards is best supported by a model having an Akaike weight of 100% (Appendix 4). The variables best explaining detection probability for the wall lizards in 2013 were stone temperature and cloud cover, whereby the quadratic effects of both variables were not significant (Table 6). Furthermore, it included connectivity, structure length and structure height as variables best explaining wall lizard abundance (Table 6). Predicted detection probability is positively affected by stone temperature (Figure 9A), whereas cloud cover influenced detectability negatively (Figure 9B).

Table 6 Beta estimates and p-values of explanatory variables included in the best *a priori* candidate abundance model for the wall lizard. Since the data have been standardized, the estimates are directly comparable to each other.

Parameter	Explanatory variable	Estimate	Std. Error	p-value
abundance	intercept	0.038	0.241	0.874
	connectivity	0.860	0.106	<0.001
	structure length	0.380	0.054	<0.001
	structure height	0.642	0.216	0.003
	structure height^2	-0.135	0.104	0.194
detection probability	intercept	-1.284	0.301	<0.001
	cloud cover	-0.499	0.154	0.001
	cloud cover^2	-0.112	0.205	0.586
	stone temperature	0.411	0.151	0.007
	stone temperature^2	0.045	0.112	0.690

The number of sand lizards observed at one structure during 2013 ranged from 0 to 14 individuals. The mean abundance estimated by using the best model accounting for detection probability was $\hat{\lambda}$=1.51 (±0.193) individuals per site. Wall lizard abundance was positively and significantly influenced by the connectivity of a site (Figure 10A). Moreover, abundance is predicted to increase with structure length and structure height, whereby the quadratic effect of height is not observable, as this effect is not significant (Figure 10B).

Removing the quadratic effect of height would lead to a slightly better model, whereas removing the other variables explaining abundance would result in higher AICc values, especially when removing connectivity (Appendix 5).

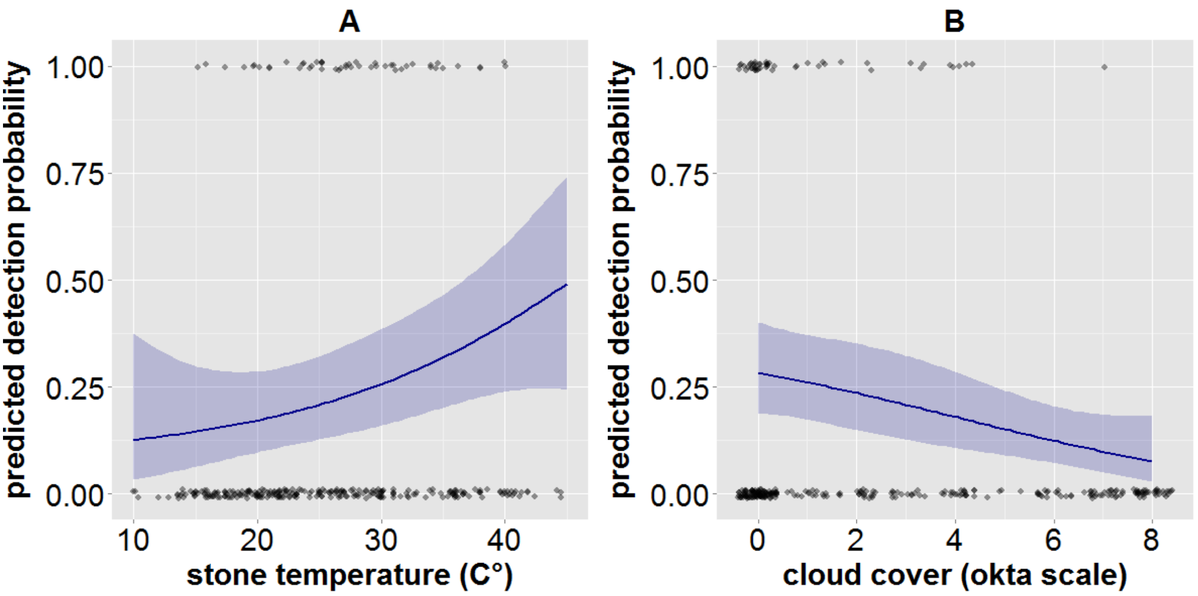

Figure 9 The effect of Stone temperature (A) and cloud cover (B) on the detectability of individuals of the wall lizard based on the best abundance model (blue line). The blue area represents the 95% confidence interval.

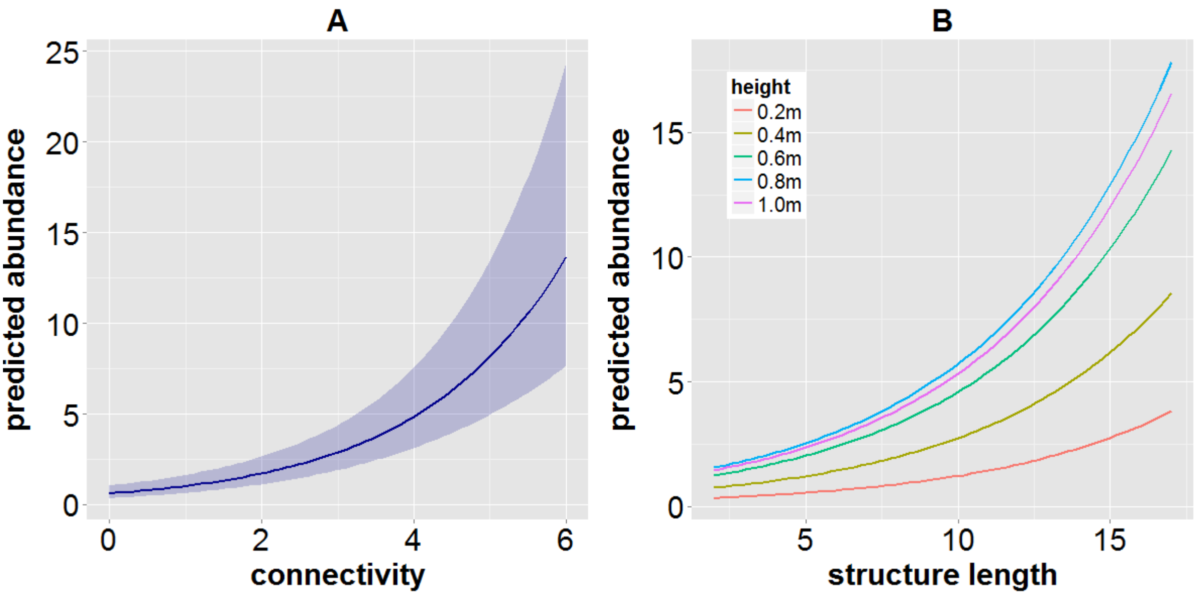

Figure 10 The effect of connectivity on the abundance of wall lizards predicted by the best abundance model (A). The blue area represents the 95% confidence interval. Plot B shows that the predicted wall lizard abundance is influenced positively by structure length and structure height.

4. Discussion

This study aimed at improving conservation action using an evidence-based approach by assessing the benefits of a reptile habitat management strategy, namely the construction of artificial stone structures as a way of enhancing potential reptile habitats. We performed a multi-season occupancy and an abundance study at stone structures on railway embankments in northern Switzerland. Our results showed that the proportion of sites occupied by the two species, *Lacerta agilis* and *Podarcis muralis*, remained largely unchanged between 2007 and 2013. Sand lizard occupancy was estimated at more or less 50% in both 2007 and 2013, whereas wall lizards occupied around 30% of the surveyed structures. These results suggest that the colonisation process of the stone structures must have been largely completed by 2007.

4.1. Detection probability

Imperfect detection is a major problem which occupancy and abundance studies need to take into consideration (Kéry 2002, MacKenzie et al. 2003, Royle and Nichols 2003, Tyre et al. 2003). Failing to account for it would lead to largely underestimated occupancy and abundance and consequently to false implications. The results of our analysis show that the probabilities to detect both species on stone structures are strongly affected by the stone temperature. For both species, detectability was highest at mean stone temperatures around 30°C and decreased with lower and higher temperatures (Figures 3A & 5A). It should be noted that the structure surface offers a range of different surface temperatures, as the stones are not equally exposed to the sun. Moreover, single temperature measurements of stone surfaces on which sand lizards were observed to bask indicate a preference of surface temperatures of around 27°C (personal observations), which is congruent to findings in House et al. (1980), who observed mean basking temperatures of 26.3°C for sand lizards. Wall lizards seem to be more tolerant to higher temperatures (personal observation). Avery (1978) showed that wall lizards try to maintain body temperatures ranging from 33 – 36°C. These higher preferred body temperatures for the wall lizard may explain the linear rather than concave trend between detectability of wall lizard individuals and stone temperature yielded from the best abundance model (Figure 9A) as well as their significant reaction to cloud cover in terms of being more exposed to the sun and therefore more detectable when cloud cover is low (Figure 9B).

Activity patterns of lizards and therefore also the detectability is strongly influenced by the ambient and surface temperature. As a result of changing temperatures, reptiles show thermoregulatory behaviours (Castilla et al. 1999) such as exposing themselves to solar radiation to raise their body temperature or using shelters for cooling down (House et al. 1980, Edgar et al. 2010). By switching between different microhabitats, reptiles manage to maintain optimal body temperatures for most of the day (Edgar et al. 2010). An ideal lizard habitat thus needs to provide different microhabitats by containing a mosaic of open areas and shelter from the elements as many works already underlined (House and Spellerberg 1983, Hofer et al. 2001, Edgar et al. 2010). Stone structures fulfil these requirements as they provide both basking areas as well as a hiding place.

Detectability for sand lizards was additionally affected by the visit duration. According to the best multi-seasonal model which analyses data from both 2007 and 2013, the probability to detect a sand lizard population is predicted to rise with increasing amount of time spent at a site (Figure 3B), which is what one would expect. Conversely, our best sand lizard abundance model, which only considers data from 2013, reveals a negative relationship between detectability of sand lizard individuals and visit duration (Figure 7B). This suggests that the presence of an observer could have some disturbance effect on individuals decreasing their individual detectability.

The best sand lizard abundance model also predicts individuals of the sand lizard to be more detectable around mid-day (Figure 7A). Our best sand lizard occupancy model predicts an increasing detectability during the morning and decreasing detection probability during the afternoon. At warm, sunny days, however, we would expect to see a detectability peak in the morning and one in the afternoon with an inactivity period around mid-day (House et al. 1980). One possible explanation could be of statistical nature: the inclusion of a quadratic term for the time of the day in the model does not allow for a bimodal activity pattern to be graphed and automatically leads to a peak around mid-day. On the other hand, the stone temperatures recorded at sampling occasions, at which sand lizards were detected around mid-day, do not exceed 36°C. This is because sampling occasions around mid-day were only carried out if the weather was favourable at that time of the day. In contrast to the mornings and afternoons this consequently leads to a lower number of occasions carried out around mid-day and a higher proportion of “successful” sampling occasions.

Of course, the time of the day only represents an indirect effect on detection probability and activity patterns are strongly dependent on weather conditions. House et al. (1980) studied daily activity patterns of sand lizards and observed a basic bimodal pattern at sunny, clear days, while no clear activity pattern was observed at days with changeable weather. During early spring and autumn days as well as days with alternating sunny and overcast periods, it is absolutely possible that sand lizards show increased activity around mid-day. At very hot, sunny days, sand lizards usually avoid being exposed to the sun around mid-day to avoid overheating (House et al. 1980, Heym et al. 2013).

4.2. Factors affecting initial occupancy

Habitat restoration and enhancement are crucial to reptile conservation, but may not be sufficient to ensure colonisation or to maintain stable populations over a long period of time. In this study, connectivity overshadowed the effect of all other covariates on occupancy. Our results showed that predicted initial occupancy rised rapidly with increasing connectivity for both species, underlining the importance of this variable. Mean connectivity values for structures occupied by the sand lizards are higher than for the unoccupied ones (Appendix 6). The best occupancy model for sand lizards predicts a strong increase in predicted occupancy probability already at low connectivity values (Figure 4A). The striking effect of connectivity on the initial occupancy by the wall lizard is particularly clear, though beta estimates were unusual high and the standard errors even higher. However, all structures occupied by wall lizard were to some extent connected to neighbouring wall lizard occurrences and all unoccupied structures show connectivity values equal to zero (Appendix 6). The same pattern is true for 2013. The fact that the occupancy is much more dependent on the presence and distance to neighbouring populations than on variables reflecting habitat quality indicates that connectivity is essential for artificially created habitats to be colonised.

Many researchers stress the importance of sites being well connected in order to provide dispersal and therefore recolonisation in case of local extinction (Hanski 1994, Haddad and Tewksbury 2006, Kindlmann and Burel 2008). Our results show a strong relatedness between connectivity and occupancy and underline the importance of connectivity in a conservation framework. As suitable as a stone structure or a specific embankment may be, one of the most important preconditions for being occupied by a lizard species is its connectivity to other potential source populations. Especially in areas dominated by agricultural landscapes, dense forests or residential areas, lizard populations are largely restricted to road and rail embankments and therefore the focus should be on improving the connectivity between populations situated along embankments. Since reptiles can disperse only over short distances (Edgar et al. 2010), suitable artificial habitats should not be too far away from each other and the embankment sections lying between them should be managed in such a way as not to represent a dispersal barrier for reptiles but a potential corridor. This calls not only for a constant management of the actually artificially enhanced embankment sections and the contained stone structures, but also for a favourable management of intervening sections, which would allow movements between sub-populations.

The best sand lizard multi-season occupancy model additionally contained inclination as a linear and quadratic effect, although the effect was not significant (Figure 4B). The activity time of lizards is strongly affected by the exposition and inclination, as they affect the insolation angle and thus the microclimatic conditions of a site (Märtens et al. 1997). It could be possible that a moderate inclination provides more suitable microclimatic conditions than flat or steep embankments. According to Podloucky (1988), an optimal sand lizard habitat is characterized, among other things, by an inclination of 20-40° and a southern exposition.

4.3. Factors affecting abundance

Connectivity is also significantly affecting abundance of both species. Possibly, the same mechanisms as for the effect on occupancy are involved. However, while the predicted occupancy probability for both species already strongly increased at low connectivity values, the abundance for both species was predicted to only slowly increase at low connectivity values and showed a faster increase at higher connectivity values (Figure 8A & 10A). This suggests that although there is already a higher probability for a site to be colonised at low connectivity, individual densities increase only at higher connectivity values. One possible explanation for this is that single individuals might continually immigrate to a site with low connectivity, but in order to build up a stable population with a high number of individuals, immigration rates must not be lower than emigration rates. This implies the site to be well connected with multiple neighbouring suitable sites and thus with multiple potential source populations.

According to metapopulation models, it is expected that increased connectivity and thus increased frequency of disperser between habitats has a positive impact on population persistence and size (Haddad and Tewksbury 2006). In fact, in a study on butterfly populations, Matter et at. (2009) observed an increase in the number of immigrants to a meadow and abundance of butterflies with meadow connectivity. Moreover, Shahanan et al. (2011) described that an increased connectivity in combination with patch area leads to an enhanced bird abundance in urban revegetation. Since population size is correlated with viability, as larger populations are less susceptible to extinctions (Hanski 1994), we can reasonably infer that connectivity also contributes to the “health” of a lizard population. In a conservation point of view, artificial reptile habitats along embankments should not only be large enough to be able to support large populations but they should also be connected well enough to keep high numbers of individuals and prevent local extinctions.

The presence of wall lizards seemed to have an effect of sand lizard abundance, too. The increase in sand lizard abundance with increasing connectivity is suppressed when wall lizards are present, while at structures where only sand lizards occur, their abundance clearly increases with connectivity (Figure 8B). This corresponds to field observations, according to which at structures where both species occurred, sand lizards were much less abundant than at structures where only sand lizards occurred (personal observations). Although this result indicates that there could be some kind of competition between the two species, further work is needed to provide empirical evidence for that.

Heym et al. (2013) observed a strong overlap in microhabitat use between introduced wall lizard and native sand lizard populations, which could lead to a competitive situation between the two species. Wall lizards have much higher population densities than sand lizards (Hofer et al. 2001, Schulte et al. 2008, Heym et al. 2013), which could make them strong competitors for basking and hiding places. Moreover, due to their similar preference for insects, they could also compete for food (Schulte et al. 2008). Thanks to its ability to climb vertical surfaces and its rapid movements, we would again expect the wall lizard to outcompete the rather plump sand lizard in regard to foraging activities (Schulte et al. 2008). However, while a competition for microhabitats is conceivable, a competition for food is unlikely as there probably are differences in the choice of prey (Hofer et al. 2001, Schulte et al. 2008).

It is highly debated whether sand lizards are being displaced by introduced wall lizards, as there is still no empirical evidence for it. Several studies studying the impact of the introduced wall lizard on native sand lizard and common lizard (*Zootoca vivipara*) populations link an observed decrease in native lizard populations to a simultaneous increase in the abundance of wall lizards (Mole 2008, Schulte et al. 2008). However, it is unclear whether instead other factors like ongoing urbanisation, vegetative succession or predation by cats might lead to decreasing sand lizard populations (Schulte et al. 2008). Wall lizards might just profit from declining sand lizard populations without having a direct impact on them (Christian Mayer, personal communication).

Our study indicated a negative impact of wall lizard occurrence on sand lizard abundance and if this was really the case, stone structures should be constructed and managed in such a way that especially sand lizards benefit from them. As sand lizards prefer woody surfaces for basking (Blanke 2010) we can conclude that the construction of woody structures, instead of stone structures, would be more beneficial for sand lizards than it would be for wall lizards.

Wall lizard abundance was further affected by structure features like structure length and height, the latter having a non-significant quadratic effect (Figure 10B). The longer or higher a structure has been, the more wall lizards were observed. Wall lizards seem to be more tolerant towards conspecifics as individuals were observed to bask quite close to each other, in contrast to sand lizards, which rarely share basking places (House et al. 1980). This results in a higher number of individuals concentrated in an area a higher number of individuals using a stone structure for basking activities, which increases as the structure surface grows.

4.4. Conclusions and management implications

To meet long-term conservation objectives, a combined approach where both connectivity and habitat size and suitability are enhanced along railway embankments is needed. The placement of stone structures along railways can be judged being effective as lizards colonise and actively use them. Our study showed that connectivity not only increased the chance for a stone structure to be occupied, but also led to a higher abundance of a species. Thus, if the placement of stone structures aimed at supporting populations of a certain species, then the focus for this habitat management action should be on sites with high connectivity values. Thanks to powerful GIS tools and distribution data, the connectivity of certain sites to neighbouring populations can easily be computed.

Dispersal along railways is particularly effective in lizards (Podloucky 1988), thus there is a probability that the majority of the man-made habitats on embankments will be occupied by reptiles sooner or later. In doing so, stone structures can be used as stepping stones and facilitate dispersal between populations along railway embankments, given that the intervening sections do not constitute a dispersal barrier for any reasons and the structures do not lie too far away from each other. This is particularly essential in highly urbanized areas where lizard populations are strongly fragmented and where embankments of low intensity use play an important role as potential habitat and dispersal corridor. In this regard, we support the further placement of stone structures all along embankments, as they can be used as both small-scale habitat and stepping stones for dispersal, especially in urbanized areas where corridors are scarce. Moreover, we also encourage a reptile friendly management of intervening sections as intensively used embankments could represent dispersal barriers.

Habitat suitability also influences population viability and persistence. Reptiles are ectothermic animals. To achieve an effective thermoregulation, reptiles need different microclimatic conditions, which can be provided by varied topography, structural elements and a mixture of open areas and vegetation cover. Stone structures are best built at sunny places. The focus should be on southern exposed, moderately inclined embankments. Furthermore, the structures should be continually managed to avoid a complete overgrowth of the structure by vegetation. If structures were built to specifically support sand lizard populations, it is more recommended to use woody instead of stony structures (Blanke 2010). Furthermore, the length of a structure influenced the abundance of wall lizards but play an unimportant role for sand lizards. The circumference of a structure should instead be maximized as sand lizards preferably bask at the border regions in partial vegetation cover. Moreover, it is conceivable that sand lizards prefer flat rather than high structures due to their limited climbing ability, while wall lizards could get along quite well with higher vertical structures.

4.5. Further work

Besides the variables affecting occupancy and abundance, this study also aimed at finding variables influencing extinction and colonisation probabilities. At this point, our data on colonisation and extinction events were insufficient to detect an effect. In a continuation of this work, it would be interesting to see if an effect of variables on colonisation and extinction would be found by adding data from further years. Additionally, it would be interesting to see whether our occupancy and abundance model applies to other stone structures which were not examined in this study. Finally, more research is needed to find empirical evidence for negative effects of the introduced wall lizard on native sand lizards. In this study, sand and wall lizards occurred together at only two sites in 2007 and one site in 2013. Further studies aiming at exclusively investigating the effect of introduced wall lizard populations on native sand lizards clearly need a larger sample of sites with the two species co-occurring.

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6. Appendices

Appendix 1 This table shows the covariates used in the analysis. Habitat variables and yearly changing habitat variables were recorded once for each of the stone structures. Observation variables were recorded at each sampling occasion. Note that all covariates were used in the stepwise analysis, whereas only part of them, the ones we were more interested to know whether they have an effect on our parameters, were incorporated in the candidate models shown in Tables 1 and 2.

Observation Variables	**Measurement**	**Mean ±SD**
Date	days starting from 1.1.2013	198 ±35.5
Time of day	minutes starting from 00.00	687 ±175.4
Visit duration	minutes	6 ±2.6
Cloud cover	oktas (0/8 – 8/8, 0=no clouds, 8=no blue sky)	3 ±3
Wind strength	beaufort scale (1-7, 0= <1km/h, 7= 50-61 km/h)	2 ±1
Rainfall in previous 24 hours	yes= 1 / no= 0	-
Stone temperature	°C	22.5 ±7.3
Habitat Covariates	**Measurement**	**Mean ±SD**
Length of the structure	meters	4.14 ±2.35
Height of the structure	meters	0.39 ±0.19
Average stone diameter	meters	0.39 ±0.15
Shape of the structure	irregular=1 / regular=0	-
Presence of sand	yes= 1 / no= 0	-
Embankment exposure	E=0.4/SE=0.8/S=1.0/SW=0.6/W=0.2	-
Embankment inclination	degrees	25 ±15
Surrounding vegetation type	fertilized grass=0 / unfertilized grass=1	-
Rubus sp. density	% area covered within 3m radius around the structure (1= >50%, 0= <50%), recorded at last occasion (mid July)	-
Presence of vegetation cover on structure	present=1 / absent=0	-
Amount of vegetation cover on structure	% of the structure covered by vegetation, recorded at last occasion (mid July)	47 ±39
Structures in a 50m-buffer	number of other structures in a 50m-buffer around the structure	2 ±2
Connectivity	Si = S pj exp (-αdij) (Hanski, 1994), calculated using sightings within a 2km buffer around the site	1.25 ±1.82 (*L.a.*) 1.02 ±1.66 (*P.m.*)

Yearly changing Variables	**Measurement**	**Mean ±SD**
Average vegetation height	meters, average vegetation height over all occasions	39.3 ±24.73 (2007) 71.5 ±28.28 (2013)
Average vegetation density	%, average density over all occasions	0.8 ±0.15 (2007) 0.9 ±0.12 (2013)
Presence of sand lizards	detected at least once= 1 / never detected= 0	-
Presence of wall lizards	detected at least once= 1 / never detected= 0	-
Age of the structure	years	4.3 ±2.93 (2007) 10.3 ±2.93 (2013)

Appendix 2 The five top ranked multi-season occupancy models for both study species. df are the degrees of freedom and ω is the Akaike weight of the model. cloud = cloud cover, dur = visit duration, Stemp = stone temperature, age = age of the structure, conn = connectivity, diam = stone diameter, incl = embankment inclination, pr_La = presence of sand lizards, pr_Pm = presence of wall lizards, pr_vegcov = presence of vegetation cover.

Nr.	**Model**	**df**	**AICc**	**ΔAICc**	**ω**
Lacerta agilis					
13	$\psi(\text{conn} + \text{incl} + \text{incl}^2)\ \gamma(.)\ \varepsilon(.)$ $\rho(\text{Stemp} + \text{Stemp}^2 + \text{dur})$	10	600.3	0.00	0.620
1	$\psi(\text{conn})\ \gamma(.)\ \varepsilon(.)$ $\rho(\text{Stemp} + \text{Stemp}^2 + \text{dur})$	8	602.4	2.15	0.212
20	$\psi(\text{pr\_Pm} + \text{diam} + \text{diam}^2)\ \gamma(.)\ \varepsilon(.)$ $\rho(\text{Stemp} + \text{Stemp}^2 + \text{dur})$	10	603.3	3.07	0.133
26	$\psi(\text{diam} + \text{diam}^2 + \text{pr\_vegcov})\ \gamma(.)\ \varepsilon(.)$ $\rho(\text{Stemp} + \text{Stemp}^2 + \text{dur})$	10	608.6	8.33	0.010
16	$\psi(\text{age} + \text{age}^2 + \text{diam} + \text{diam}^2)\ \gamma(.)\ \varepsilon(.)$ $\rho(\text{Stemp} + \text{Stemp}^2 + \text{dur})$	11	609.3	9.03	0.007
Podarcis muralis					
1	$\psi(\text{conn})\ \gamma(.)\ \varepsilon(.)$ $\rho(\text{Stemp} + \text{Stemp}^2 + \text{cloud} + \text{cloud}^2)$	9	383.9	0.00	0.571
12	$\psi(\text{conn} + \text{pr\_vegcov})\ \gamma(.)\ \varepsilon(.)$ $\rho(\text{Stemp} + \text{Stemp}^2 + \text{cloud} + \text{cloud}^2)$	10	386.5	2.65	0.152
9	$\psi(\text{conn} + \text{pr\_La})\ \gamma(.)\ \varepsilon(.)$ $\rho(\text{Stemp} + \text{Stemp}^2 + \text{cloud} + \text{cloud}^2)$	10	386.5	2.65	0.152
13	$\psi(\text{conn} + \text{incl} + \text{incl}^2)\ \gamma(.)\ \varepsilon(.)$ $\rho(\text{Stemp} + \text{Stemp}^2 + \text{cloud} + \text{cloud}^2)$	11	389.3	5.38	0.039
8	$\psi(\text{conn} + \text{age} + \text{age}^2)\ \gamma(.)\ \varepsilon(.)$ $\rho(\text{Stemp} + \text{Stemp}^2 + \text{cloud} + \text{cloud}^2)$	11	389.3	5.39	0.039

Appendix 3 The top ranked multi-season occupancy model (bold*)* for both species together with its reduced models (below) to evaluate the importance of explanatory variables. The best ranked model from the stepwise approach was added at the top for comparison. The models were ranked according to their AICc-value. df are the degrees of freedom and logLik is the log-Likelihood of the model. cloud = cloud cover, dur = visit duration, Stemp = stone temperature, wind = wind strength, conn = connectivity, diam = stone diameter, incl = embankment inclination, length = structure length.

	Model	**df**	**logLik**	**AICc**	**ΔAICc**
Lacerta agilis					
Stepwise	ψ(conn +conn^2 +diam +length) γ(.) ε(.) ρ(Stemp+Stemp^2 +dur)	11	-275.7	577.5	-22.8
Best model	**ψ(conn +incl +incl^2) γ(.) ε(.) ρ(Stemp+Stemp^2 +dur)**	**10**	**-288.4**	**600.3**	**0.0**
-incl^2	ψ(conn +incl) γ(.) ε(.) ρ(Stemp+Stemp^2 +dur)	9	-288.9	598.6	-1.7
-incl	ψ(conn) γ(.) ε(.) ρ(Stemp+Stemp^2 +dur)	8	-292.1	602.4	+2.1
-conn	ψ(incl +incl^2) γ(.) ε(.) ρ(Stemp+Stemp^2 +dur)	9	-301.7	624.2	+23.9
Podarcis muralis					
Stepwise	ψ(conn) γ(.) ε(.) ρ(Stemp+Stemp^2 +cloud +cloud^2)	9	-181.6	383.9	0.0
Best model	**ψ(conn) γ(.) ε(.) ρ(Stemp+Stemp^2 +cloud +cloud^2)**	**9**	**-181.6**	**383.9**	**0.0**
-conn^2	ψ(.) γ(.) ε(.) ρ(Stemp+Stemp^2 +cloud +cloud^2)	8	-229.6	477.4	+93.5

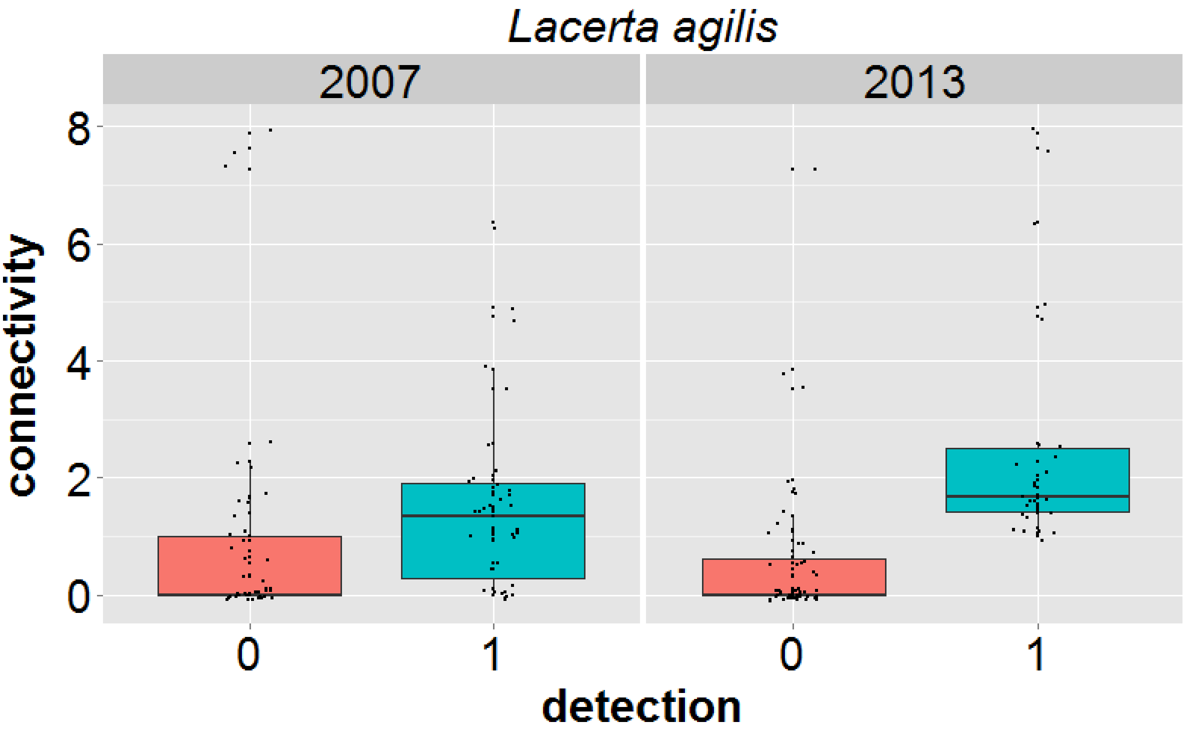
Appendix 4 The five top ranked abundance models from the candidate model list for both study species. df are the degrees of freedom and ω is the Akaike weight of the model. cloud = cloud cover, dur = visit duration, Stemp = stone temperature, time = time of day, age = age of the structure, conn = connectivity, diam = stone diameter, height = structure height, incl = embankment inclination, length = structure length, pr_La = presence of sand lizards, pr_Pm = presence of wall lizards, vegcov = amount of vegetation cover.

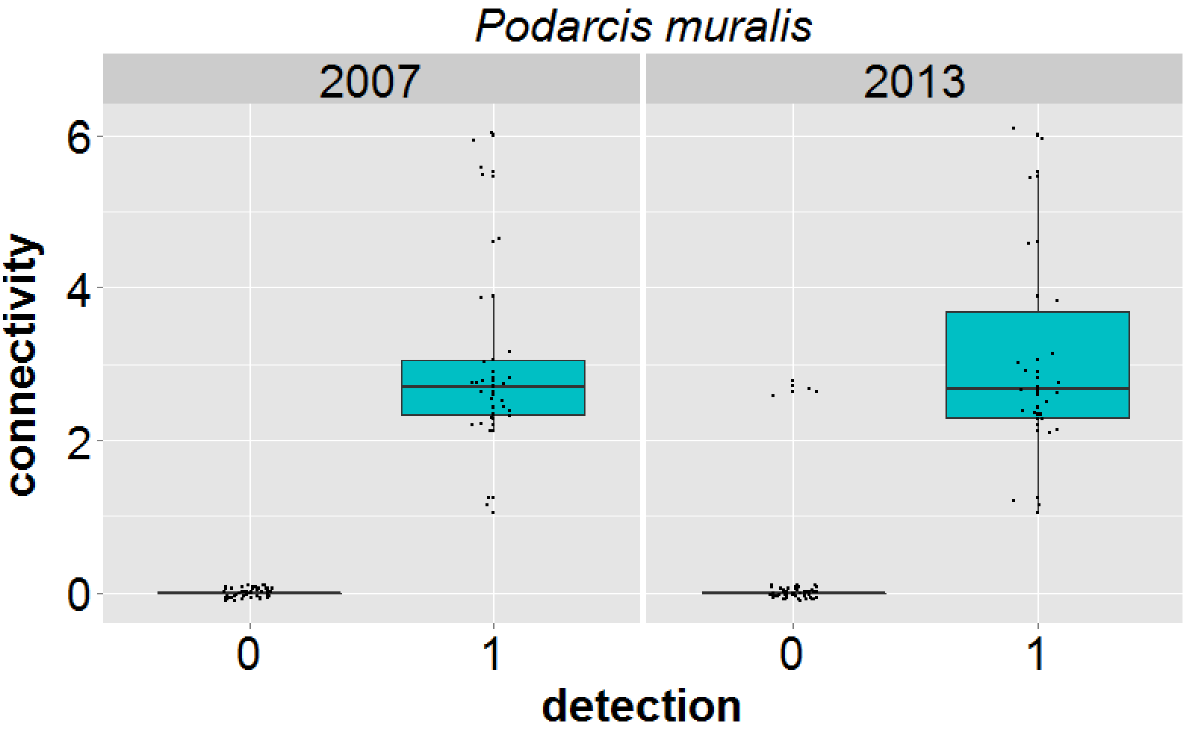
Nr.	**Model**	**df**	**AICc**	**ΔAICc**	**ω**
Lacerta agilis					
9	λ(conn +pr_Pm) ρ(dur +time +time^2)	7	402.9	0.00	0.829
27	λ(diam +diam^2 +incl +incl^2) ρ(dur +time +time^2)	9	408.1	5.16	0.063
22	λ(pr_Pm +incl +incl^2) ρ(dur +time +time^2)	8	408.2	5.28	0.059
20	λ(pr_Pm +diam +diam^2) ρ(dur +time +time^2)	8	408.8	5.89	0.044
28	λ(vegcov +vegcov^2 +incl +incl^2) ρ(dur +time +time^2)	9	414.4	11.48	0.003
Podarcis muralis					
10	λ(conn +length +height +height^2) ρ(Stemp +Stemp^2 +cloud +cloud^2)	10	434.0	0.00	1.000
12	λ(conn +vegcov +vegcov^2) ρ(Stemp +Stemp^2 +cloud +cloud^2)	9	465.1	31.12	0.000
15	λ(age +age^2 +length +height +heigth^2) ρ(Stemp +Stemp^2 +cloud +cloud^2)	11	478.6	44.61	0.000
9	λ(conn +pr_La) ρ(Stemp +Stemp^2 +cloud +cloud^2)	8	489.2	55.25	0.000
24	λ(length +height +height^2 + vegcov +vegcov^2) ρ(Stemp +Stemp^2 +cloud +cloud^2)	11	495.4	61.41	0.000

Appendix 5 The top abundance model from the candidate model list (bold) for the both species with its reduced models (below) to evaluate the importance of explanatory variables. The best ranked model from the stepwise approach was added at the top for comparison. The models were ranked according to their AICc-value. df are the degrees of freedom and logLik is the log-Likelihood of the model. dur = visit duration, time = time of day, Stemp = stone temperature, cloud = cloud cover, age = age of the structure, conn = connectivity, exp = embankment exposition, incl = embankment inclination, height = structure height, length = structure length, vegcov = amount of vegetation cover.

	Model	**df**	**logLik**	**AICc**	**ΔAICc**
Lacerta agilis					
Stepwise	λ(conn +conn^2 +incl +incl^2 +age +age^2 +exp) ρ(dur +time +time^2)	12	-148.5	326.0	-76.9
Best model	**λ(conn +pr_Pm)** **ρ(dur +time +time^2)**	**7**	**-193.6**	**402.9**	**0.00**
-pr_Pm	λ(conn) ρ(dur +time +time^2)	6	-214.2	441.6	+38.7
-conn	λ(pr_Pm) ρ(dur +time +time^2)	6	-209.0	431.3	+28.4
Podarcis muralis					
Stepwise	λ(conn +conn^2 +vegcov +vegcov^2 +incl) ρ(Stemp +Stemp^2 +cloud +cloud^2)	11	-161.2	348.6	-85.4
Best model	**λ(conn +length +height +height^2)** **ρ(Stemp +Stemp^2 +cloud +cloud^2)**	**10**	**-205.3**	**434.0**	**0.00**
-height^2	λ(conn +length +height) ρ(Stemp +Stemp^2 +cloud +cloud^2)	9	-206.2	433.2	-0.8
-height	λ(conn +length) ρ(Stemp +Stemp^2 +cloud +cloud^2)	8	-210.5	439.1	+5.1
-length	λ(conn +height +height^2) ρ(Stemp +Stemp^2 +cloud +cloud^2)	9	-228.1	476.9	+42.9
-conn	λ(length +height +height^2) ρ(Stemp +Stemp^2 +cloud +cloud^2)	9	-239.6	499.9	+65.9

Appendix 6 Boxplots showing the distribution of connectivity values among sites at which lizards were detected (1) or not detected (0). The mean connectivity of unoccupied sites is for both species lower than the mean connectivity of the occupied sites. For the wall lizards, the unoccupied sites had nearly all a connectivity value of zero.





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I declare that I have used no other sources and aids other than those indicated. All passages quoted from publications or paraphrased from these sources are indicates as such, i.e. cited and/or attributed. This thesis was not submitted in any form for another degree or diploma at any university or other institution of tertiary education.

Zurich, 20.02.2014

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