How site characteristics, competition and predation influence site specific abundance of sand lizard on railway banks

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Abstract

Whereas many natural habitats have been or are being destroyed, other habitats are created. Man-made habitat can be very important for rare and endangered species. Particularly relevant for conservation are reptiles because they are very sensitive to habitat degradation. Still, relatively high abundances of certain reptiles can be found on suitable man-made habitats such as railway banks. Especially associated with railway bank habitats is the sand lizard (*Lacerta agilis*). However, it is unknown which abiotic site characteristics of railway banks match the niche requirements of *L. agilis* and therefore allow it to maintain high abundances. Further it is also important to recognise that interspecific competition with the common wall lizard (*Podarcis muralis*) and predation, mainly through domestic cats (*Felis catus*), may also account for some of the observed variation in abundance. In our study we examined the effect of site characteristics, competition and predation on the abundance of *L. agilis* on railway banks. The study, conducted in the Swiss lowlands, included replicated counts of *L. agilis*, *P. muralis* and domestic cats in 50 sites on railway banks. To examine site characteristics we recorded exposition, management regime, soil characteristics, cover of different habitat structures, vegetation composition, and derived bio-indicators, such as plant diversity and Landolt indicator values. We accounted for imperfect detection trough the incorporation of observation covariables and detection probabilities. We tested the effect of site characteristics, competition, and predation using a candidate and a stepwise model selection approach. The mean detection probability was 0.14. The selected best model incorporated 15 explanatory variables. Railway banks which are cut early in the year, south facing and which provide a minimal number of rodent holes and only a low cover of thorn stands can host high abundances of *L. agilis*. Still of intermediate importance were herbaceous vegetation height and cover as well as the equitability of the vegetation composition. Also, railway banks should consist of very sandy soil. Further it is important that the habitat offers a large temperature gradient in a small area. However, our results indicate that not a single element but a combination of different site characteristics determines high abundances of *L. agilis* on railway banks. We could not find any effect of competition with *P. muralis* or the presence of domestic cats on the the abundance of *L. agilis.* Our study improves the general knowledge about the habitat requirements of *L. agilis* and it leads to management strategies that will improve the railway banks as habitats for *L. agilis*. Due to the ongoing loss or degradation of reptile habitats, railway banks can be of great value for conservation if they provide the required site characteristics. Our study indicates that such man-made habitats can be important elements in an intensively exploited landscape, which may also be true for other species.

Introduction

It is a fundamental goal of ecological research to understand how site characteristics influence spatial variation in abundance (Begon et al. 2006). We assume that the niche of each species consists of multiple, independent factors that limit the fitness of individuals and hence abundance and distribution of populations (Brown et al. 1995). The simulations of Brown et al. (1995) suggest that most of the spatial variation in abundance of many species might be explained by the extent to which local environmental conditions meet a modest number of niche requirement.

In human-dominated landscapes many natural habitats have been destroyed, causing a drastic decline in the abundance and distribution of many species. The loss of habitats does not only include the destruction itself, but also damage associated with habitat degradation, and fragmentation (Primack 2006). In future, land-use change and the associated habitat alteration will continue to be the main factor affecting biodiversity in terrestrial ecosystems (Tilman et al. 2001).

However, at the same time many species thrive in novel habitats that were created by humans. For instance, through the construction of transport axes, new habitats on banks of railways have been generated. And, at least in Middle Europe, railway banks cover great surfaces. In an over-exploited landscape, extensively used railway banks can offer potential habitats for many species. Because of the overlap of different landscape elements and the broad spectrum of different microclimates, the diverse site characteristics allow many species to reach high abundances (Carthew et al. 2013, Rotholz and Mandelik 2013). If some of those are endangered or rare species, railway banks can have high conservation values. It is therefore important to know which site characteristics of railway banks determine the occurrence and hence abundance of rare or endangered species.

One group of organisms particularly relevant for conservation are reptiles because many reptile species are declining (Böhm et al. 2013). Among the main threats to reptile populations are habitat loss and degradation (Gibbons et al. 2000, Hofer et al. 2001, Böhm et al. 2013). However, relatively high abundance of particular reptiles can be found in suitable man-made habitats (Hofer et al. 2001). Railway banks especially seem to provide those site characteristics that allow some reptile species to cover their resource needs (Hofer et al. 2001). One reptile species that is often associated with railway bank habitats is the sand lizard (*Lacerta agilis* LINNAEUS, 1758) (Andrén et al. 1988, Bischoff 1988, Hofer et al. 2001, Kéry et al. 2009). Currently, it is unknown which site characteristics of railway banks match the niche requirements of *L. agilis* and therefore allow it to maintain high abundances. Further, railway banks are man-made surfaces, it is vital to identify the important site characteristics in order to be able to provide and maintain them.

It is also important to recognise that interspecific competition may also account for some of the observed variation in abundance (Brown et al 1995). Experts assume that *L. agilis* is additionally losing potential habitats due to the competition with the common wall lizard (*Podarcis muralis* LAURENTI, 1768) (A. Meyer, personal communication). As reported by Hofer et al. (2001), the niches of *L. agilis* and *P. muralis* overlap in the Swiss lowland by 34 %. Whereas *L. agilis* only shares 1 % of their occupied habitats with *P. muralis*, *L. agilis* is present in 29 % of the *P. muralis* habitats. The effect of the interspecific competition on the abundance of *L. agilis* has not been studied so far.

Moreover *L. agilis* suffers from predation through domestic cats (*Felis catus*) (Hofer 1998). As a pet animal, the domestic cat can attain very high densities and has the potential to exert detrimental effects on prey species, among other wildlife species also on reptile species (Woods et al. 2003). Experts believe that a locally high abundance of domestic cats can reduce the abundance of *L. agilis* greatly (A. Meyer, personal communication). When estimating the abundance of *L. agilis* it is therefore important to account additionally for the presence of domestic cats as an indicator for predation.

In our study we examined the effect of site characteristics, competition and predation on the abundance of *L. agilis* on railway banks. Our specific goals were to identify abiotic and biotic explanatory variables or a priori defined groups of explanatory variables which can best explain the site specific abundance of *L. agilis*.

Material and methods

Study species

The potential area of distribution of *L. agilis* would include broad parts of the European lowlands (Blanke 2010). Because of the intensification of agricultural production, the actual area of distribution is nowadays often restricted to man-made habitats (Hofer 1998, Monney and Meyer, 2005). Because populations of *L. agilis* declined 11.2 % between 1980 and 2004, *L. agilis* is listed as vulnerable in the Swiss Red List (Monney and Meyer, 2005).

As an ectotherm animal, *L. agilis* can exploit complex microclimatic mosaics to regulate its body temperature behaviorally (Bogert 1949). It requires low-shade environments for basking, and areas of shade or below ground holes to cool down if air temperatures are too high (Kearney et al. 2009). The efficacy of behavioral thermoregulation is tied to the availability of shade, and hence to the nature and extent of vegetation cover (Kearney et al. 2009). We therefore measured site characteristics such as vegetation cover, and woody or stony structures that have a high heat storage capacity and which therefore can serve as basking spots. Furthermore, the management regime was assessed because pruning the vegetation can change the local microclimate drastically and therefore alter the availability of spots for thermoregulation.

Because many site characteristics cannot be measured directly, we used vegetation data to characterize environmental variation among sites. The ecological amplitude of some plant species may reflect that of *L. agilis* (Märtens 1999). Derived bio-indicators from plant abundance data, e.g. Landolt values (Landolt 1977), allow the assessment of environmental variation that is otherwise difficult to measure (Diekmann 2003). Landolt indicator values describe the niche position of plant species for several environmental factors on an ordinal scale and are commonly used to assess habitat characteristic based on vegetation (Diekmann 2003). Of particular interest were the Landolt values for light, soil moisture and soil nutrients.

L. agilis is threatened by predation not only through domestic cats but by many other species (Blanke 2010). The availability of shelter structures is accordingly crucial for the survival of populations. We therefore estimated the availability of shelter structures such as rodent holes, litter heaps, thorn stands or piles of stones.

Another major constraint is the availability of nesting sites, in particular of sandy soils (Rykena and Nettmann 1987, Andrén et al. 1988, Bischoff 1988, Strijbosch 1988, Blanke 2010). To assess nesting sites, we estimated soil characteristics, in particular the relative content of sand, of the skeleton fractions and of humus.

Study area

The study area lies in the Swiss lowland and covers an area with a radius of approximately 30 km around the town of Berne. Elevation ranges from 440 to 790 meters above sea level. Land use in the study area is characterized by intensive agriculture and is relatively densely covered by human settlements. We restricted our study to slopes of railway lines, as they still hold strong populations of *L. agilis* (Hofer 1998). These slopes are generally subject to extensive mowing.

Site selection

Within the study area, we examined 50 sites from a total of 116 sites where *L. agilis* was observed after 1982 (Swiss Biological Records Center CSCF, 2012). Information available for these 116 sites included the number of individuals per sampling site recorded in the CSCF data base, the distance to the next sampling site and the age of record (i.e. the year when the species was last reported). We then randomly selected 50 sites which covered the entire range of number of individuals, distance and age of record. We excluded sites that were inaccessible, had a northern exposition or were shaded by buildings, hills, forests or noise protection walls. The minimal distance between two sites was 1 km. We defined a sampling site as a 100 m section of a railway slope. Site width corresponded to railway slope width and ranged between 2.9 m and 15 m (mean 6 m).

During August and September 2012, we observed young hatchlings on all sites where we also found adult individuals of *L. agilis*. Consequently reproduction was occurring on all sites that were occupied by *L. agilis*.

Lizard and domestic cat survey

We carried out a *L. agilis* survey to estimate abundance while accounting for imperfect detection. When carrying out surveys, individuals may go undetected when present for several reasons (proximity to observer, cryptic behavior or camouflage) (Kéry et al. 2009). We accounted for imperfect detection through the estimation of detection probabilities and integration of factors influencing the observation process such as weather conditions at the time of observation, observation duration, date and time of day.

Each site was visited 3 times from the end of April 2012 to the end of June 2012. During this period, detection probability is known to be high (Kéry et al. 2009) and we can assume that the populations were closed. The visits were carried out on days with weather conditions as favourable as possible for the observation of *L. agilis*, i.e. without rain, neither too cold nor too hot (around 19°C) and without strong wind (Kéry et al. 2009). During each visit, we counted all *L. agilis* along a 100 m section of a railway slope. Separate counts were made for females, males, adults with unknown sex and juveniles. At each visit, we recorded the observation covariables date, time of day and observation duration (Table 1). Meteorological data was obtained from the nearest meteorological monitoring station of the Federal Office of Meteorology and Climatology (IDAWEB database 2012) (Table 1).

Furthermore we counted the individuals of *P. muralis* using the same method as for *L. agilis*. We used the maximum value of counted adult individuals per site as an explanatory variable.

The domestic cats were counted repeatedly during each survey. We used the total number of observed domestic cats per site as an explanatory variable.

Site characteristics

Between mid-June 2012 and mid-September 2012, we recorded site characteristics at three spatial scales in order to explain variation in the abundance of *L. agilis* (Table 2).

At the site level (100 m section of a railway slope) we recorded the width of the railway slope, the exposition and the management history (month of first cut, mulching). The management history was recorded repeatedly during the site characteristics survey and the four *L. agilis* surveys.

At the 20 m sector level we estimated the ground cover of habitat structures such as herbaceous and woody vegetation, open ground, solid materials, gravel, dead wood or thorn stands. From this data we calculated the average cover of each habitat structure per site.

At the plot level we recorded the vegetation and soil characteristics at five plots (1 m^2) randomly placed in each 20 m sector. On each plot we determined all vascular plant species (excluding seedlings) and estimated their foliar cover and the ground cover (vegetation, open ground, gravel, stones) to the nearest percent for abundances below 10 % and the nearest 5 % for abundances above 10 %. From the species list we derived plant species number, the Shannon index (Begon et al. 2006) and the Shannon equitability (Begon et al. 2006) as measures of plant diversity. To assess abiotic conditions, we calculated the Landolt indicator values (Landolt 1977) for soil moisture, light, and soil nutrient, averaged over all plant species per plot using the VEGEDAZ computer program, version 02.2012 (Küchler 2009). Further we estimated the litter quantity and counted all rodent holes on the plot. We measured the height of the vegetation three times on an each time randomly placed plot between mid-May and mid-September. To obtain soil characteristics, we took a core (approximately 10 cm depth, 5 cm width) and estimated in a qualitative manner the relative content of sand, of the skeleton fractions and of humus (Brunner et al. 2002).

Statistical analyses

We checked for collinearity of explanatory variables using Pearson correlation analysis. Variables that were dropped from the analysis because they were highly correlated with others are given in

Table 2. There was no need to remove outliers. We z-standardized all continuous and categorical explanatory variables and observation covariables (Schielzeth 2010) prior to analyses. To estimate abundance and detection probabilities, we fitted N-mixture models (Royle 2004) to the replicated count data using the package unmarked (version 2.13.2) and the fitting function 'pcount' with a normal, negative binominal and zero-inflated poisson distribution (Fiske and Chandler 2011) in R (version 2.13.1) (R Development Core Team 2011). The N-mixture model is a hierarchical model that combines a submodel for the observation process with a submodel for abundance. The model integrates both observation covariables to describe detection probability during observation and explanatory variables such as the site characteristics, abundance of *P. muralis* and abundance of domestic cats to describe site-specific abundance. We integrated in our models both types of variables, either with linear or quadratic effects.

Model fitting and selection

We divided the analysis into two steps. In the first step we incorporated observation covariables for the selection of a model that best explains variation in detection probabilities. The detection probability parameter accounts for the observation process and is defined as the probability of detecting an individual that is present (Royle 2004). We fitted each observation covariable and each quadratic effect to N-mixture models and set the explanatory variable part constant. Afterwards we ranked the models by their AIC value (Burnham and Anderson 2001).

In a second step, we used the model that best explained detection probability to find a model that best explains the abundance of *L. agilis*. To model variation in abundance among sites as a function of site specific explanatory variables, we used a candidate model approach (Franklin et al. 2001) and a stepwise model selection approach. For the candidate model selection approach, we developed 16 different a priori candidate models that represent different biological working hypotheses (Table 4). Each model referred to different aspects of the biology of *L. agilis*. The development of the models was based on literature and expert knowledge. AIC was used to rank the models.

In order to further explore information in the data set, we additionally used a stepwise model selection approach. We deleted, based on AIC values, explanatory variables from a fitted model to get the most parsimonious model (Anderson et al. 1998).

Results

Detection probability

At 41 sites we detected at least one *L. agilis* during the three visits while at nine sites no *L. agilis* were detected. The model that described detection probabilities best included observation duration as a linear and quadratic effect (Table 3). All other models had considerably less support from the data (Table 3). We therefore only used the observation covariable observation duration and its quadratic effect for the further analysis. The result shows that an observer should spend about 30 minutes searching for *L. agilis* individuals at one site (Figure 1). Investing more time will not lead to a higher detection probability. Expected detection probabilities were between 0.048 and 0.2 (mean = 0.14) (Figure 1).

Estimation of site specific abundance

The candidate model which best explained the variation in site specific abundance of *L. agilis* was the model number 1 (Table 5). It included explanatory variables which specify structures used by *L. agilis* for basking; namely the exposition, the litter quantity, cover of solid materials, cover of gravel, cover of woody structures and the Landolt value for light. All other candidate models were at least 19-fold less well supported by the data than the top ranked model (Table 5).

However, the stepwise selected best model was 24 million times better supported by the data than any of the candidate models (Table 5). The best ranked model incorporated 15 explanatory variables (Table 6, Figure 2). Vegetation height, soil sand content and cover of woody structures had a positive effect on the expected abundance of *L. agilis*. The cover of thorn stands had a negative effect. The confidence interval of the estimate of the effect of open ground included zero. Exposition, month of the first cut, litter quantity, number of rodent holes, cover of woody vegetation and Shannon equitability had a convex quadratic effect on abundance. A concave quadratic effect was exhibited by slope width, cover of the herbaceous vegetation, cover of gravel and Landolt value for light.

Discussion

The estimated detection probabilities in our study are congruent with findings (probabilities between 0.05 and 0.3) of other studies (Kéry et al. 2009). These low probabilities underline that detectability, especially for reptiles, is far from perfect (Kéry 2002, Brown et al. 2007, Kéry and Schmidt 2008, Kéry et al. 2009). If we would only have integrated counts in the analysis without accounting for the observation process (mean detection probability = 0.14), we would on average have underestimated the abundance by a factor of 7. Our results show that the time spent looking for animals influenced detection probabilities most strongly. Spending approximately half an hour searching for animals resulted in the highest estimated detection probability. This suggests that an optimal observation duration exists. Searching longer will possibly create more disturbances leading to a lower detection probability. No other observation covariable, namely weather conditions, date and time of day, had an effect on the expected detection probabilities.

We tested different candidate hypotheses to check the effect of a priori defined groups of explanatory variables which represented aspects of the biology of *L. agilis*. The application of our candidate models was not successful. None of the resulting candidate models had sufficient support from the data. The expected abundance of *L. agilis* was best explained with the stepwise model approach. The selected best model consisted of a combination of 15 explanatory variables and represented a variety of aspects of the biology of *L. agilis*. The gap between those two approaches showed that abundance is determined by an interplay of many abiotic and biotic variables.

The influence of site characteristics on species abundance

The management regime had the biggest effect on the abundance of *L. agilis* (Table 6, Figure 2). Our results showed that an early cut led to higher expected abundances of *L. agilis*. In contrast, the later the cut in the year, the lower the expected abundance. No cut at all also resulted in lower abundances. We could not find an effect of the mulching on the expected abundance. It seems that cutting the vegetation early in the year changes the local microclimate in a positive way and enhances the availability of spots for thermoregulation. This effect may be caused by the lower air temperature in spring which requires *L. agilis* to catch more sun. In contrast, later in the year when air temperatures are higher, a cut might reduce the availability of shaded spots. It is known from other studies (Blanke and Podloucky 2009) that if meadows are heavily overgrazed and vegetation is consequently short and patchy, shelter structures and good opportunities for thermoregulation are lacking and abundances of *L. agilis* are low. Additionally, mowing- machines in use can directly injure or kill individual reptiles (Blanke 2010).

Another big effect was the availability of gravel and thorn stands (Table 6, Figure 2). Our results suggest that a cover of gravel lower than 8 % or higher than 30 % led to a higher expected abundance of *L. agilis*. A habitat that provides a small amount (< 10 %) of thorn stands such as roses or blackberry stands, can maintain higher abundances. However, a wide cover of thorn stands has a negative effect. We found no study which tested the effect of gravel or thorn stands to compare our results with. A study of Krug et al. (1996) showed that the spatial heterogeneity of a habitat has a major effect on the survival probability of *L. agilis* populations. The structural heterogeneity was characterized through a constant change in the height and the cover of the vegetation and spots of open ground. Our result showed an intermediate effect of the vegetation height and the cover of herbaceous vegetation and a low effect of the cover of woody vegetation. Railway banks with herbaceous vegetation between 20 to 30 cm in height which covered approximately 10 to 40 % hosted high abundances of *L. agilis*. Other studies report different vegetation heights as being optimal. Gramentz (1996) could only sporadically detect the species in areas that had a cover of vegetation lower than 25 % or higher than 90 %. Studies in Germany report that the cover of herbaceous vegetation in *L. agilis* habitats ranges from 60 to 90 % and that vegetation heights are never lower than 40 to 50 cm (Podloucky 1988, Märtens et al. 1997). The cover of woody vegetation predicted a high abundance of *L. agilis* if it was between 5 and 15 %. Higher covers of woody vegetation lead to a reduced expected abundance of *L. agilis*. Other studies report covers of shrubs of around 30 % (Podloucky 1988) or around 17 % (Schnürer et al. 2010) as being optimal for *L. agilis*. It seems that in different *L. agilis* habitat types, cover and height of herbaceous and woody vegetation can greatly vary and that no optimal mix exists.

The effect of slope exposition also played a major role (Table 6, Figure 2). On banks with an exposition south, *L. agilis* reached relatively high abundances. Our findings are consistent with the literature (Bischoff 1988, Hofer et al. 2001, Kéry et al. 2009).

Also very important are the number of rodent holes in the ground which are used by *L. agilis* as shelter structures and for thermoregulation (Table 6, Figure 2). Our data suggest that there was a need for approximately 3 rodent holes per 1 m^2 to maintain high abundances. An article by NCC (1983) points out the importance of rodent holes as shelter structures, but did not quantify this.

The Landolt value for light had an intermediate effect on the abundance of *L. agilis* (Table 6, Figure 2). To promote high abundances, the environmental conditions of light (Landolt value between 2.5 and 3) needed to be intermediate. Consequently, soil moisture, which was highly correlated with the light, also needed to be intermediate. On railway banks with a very sunny and dry microclimate, *L. agilis* abundances were low. As stated by Blanke (2010), *L. agilis* prefers habitats that exhibit high temperature gradients. Probably the light and soil moisture values indicate not only that the optimal habitat exhibits intermediate conditions but it might also indicate a range of conditions reflected in intermediate mean values.

The Shannon equitability also had an intermediate effect, but we did not found an effect of the plant species number and the Shannon index (Table 6, Figure 2). Sites which had either a higher equitability (all species occur at approximately the same frequency) or a lower equitability (only a few species occur in high frequency, all other are rather rare) exhibited a lower abundance. An optimum occurred where most species were quite common, but some are still more abundant than others.

We tested a number of soil variables, but only the soil sand content had an effect on the abundance of *L. agilis* (Table 6, Figure 2). The sandier and less humus rich the soil of railway banks, the higher was the expected abundance of *L. agilis*. The importance of sandy soil for nesting is confirmed by many studies (Rykena and Nettmann 1987, Andrén et al. 1988, Bischoff 1988, Strijbosch 1988, Blanke 2010). An effect of the skeletal content could not be found. Possibly, and independently of the abundance of *L. agilis*, all railway banks close to the rails have very skeletal rich soils.

The effect of litter quantity and woody structures was low and solid material did not have any effect (Table 6, Figure 2). If the banks provided some litter heaps that were not too large, and many woody structures such as dead wood, piles of wood or woody railway sleepers for basking, *L. agilis* could maintain higher abundances. On the other hand, the occurrence of solid materials, such as cable ducts, concrete constructions, rock surface or piles of stones did not play a role. Our findings are concurrent with former studies (House et al. 1980, Blanke 2010, Schnürer et al. 2010). As observed by Schnürer et al. (2010), *L. agilis* often bask on dry vegetation, e.g. litter, leaves or moos, which is widely abundant in habitats. Blanke (2010) pointed out that *L. agilis* clearly prefers woody basking spots and that even if widely available, stones or gravel are rarely used.

We can conclude that railway banks which are cut early in the year, south facing and which provide a minimal number of rodent holes and only a low cover of thorn stands can host high abundances of *L. agilis*. Of intermediate importance are herbaceous vegetation height and cover as well as the equitability of the vegetation composition. Also, railway banks should consist of very sandy soil. Further it is important that the habitat offers a large temperature gradient in a small area. Our results indicate that not a single element but a combination of different site characteristics determines high abundances of *L. agilis* on railway banks.

The influence of competition and predation on species abundance

Beside site characteristics, we examined the effect of competition and presence of domestic cats on the abundance of *L. agilis* on railway banks. We could not find any effect of competition with *P. muralis* or the presence of domestic cats on the the abundance of *L. agilis.* Therefore we can not confirm that *L. agilis* is losing potential habitats due to interspecific competition. Probably the two species differ in their specific resource use, e.g. prey choice, in shared habitats (Hofer et al. 2001). Further, we could not confirm that the predation through domestic cats reduces local *L. agilis* abundance. Perhaps we could not detect an effect because of methodical constraints. We only counted the number of domestic cats during the surveys and could therefore only cover a short time span and a small part of the activity area of a domestic cat. It is possible that the use of the distance between a site and the next human settlement as an explanatory variable would have been more accurate.

Conclusion

Railway banks are habitats, that are constructed and maintained by humans. Because our results show that a combination of site characteristics is crucial for high abundances of *L. agilis*, management efforts should consider a series of site characteristics rather that focusing on one single element. In order to provide optimal site characteristics for *L. agilis* the following instructions should be followed. Priority should be given to south facing slopes and slopes which are colonized by rodents. The vegetation should be cut rather early in the year. Thorn stands, shrubs, trees and litter heaps should only cover a small part of the surface, whereas herbaceous vegetation could cover up to half of it. Vegetation should reach up to 30 cm in height. Also, railway banks should consist of very sandy soil. The provision of dead wood pieces, piles of wood or woody railway sleepers is more promising than that of piles of stones.

Railway banks that provide the required site characteristics are important novel habitats for *L. agilis* in a highly human altered landscape. Due to the ongoing loss or degradation of *L. agilis* habitats, such man-made habitats are of great value for the conservation of *L. agilis* populations. Further, due to the complex requirements of *L. agilis*, optimal reptile habitats often provide suitable site characteristics for many other species (Völkl and Käsewieter 2005, Blanke and Podloucky 2009). The contribution of novel habitats to regional biodiversity conservation should therefore not be underestimated (Coffin 2007, Carthew et al. 2013). However more taxa should be studied to test whether the same heterogeneous combination of site characteristics is important for other species too. Our study indicates that novel man-made habitats can be important elements in an intensively exploited landscape and should therefore be retained and appropriately managed.

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Tables

TABLE 1. Observation covariables

Observation covariables	Mean	Used in analysis	Sampling interval	Spatial reference	Source	Measuring detail	Context / Reference
Date	60	Yes	Repeated	Site	Measure	1.4.2012 = day 1	Annual activity pattern of *L. agilis* (Kéry et al. 2009, Nuland and Strijbosch 1981)
Time of day	13.4 h	Yes	Repeated	Site	Measure	Hour and minutes (%) at begin of observation	Daily activity pattern of *L. agilis* (House et al. 1980)
Observation duration	0.35 h	Yes	Repeated	Site	Measure	Hour and minutes (%)	Observation process
Air humidity	59 %	Yes	Repeated	Region	MeteoSwiss	Mean of one hour (%), measured 2 meter above ground	Activity pattern (Expert knowledge)
Solar radiation	626 W/m	Yes	Repeated	Region	MeteoSwiss	Global (W/m), mean of one hour	Activity pattern (NCC 1983, Elbling 1997)
Air temperature	19 °C	Yes	Repeated	Region	MeteoSwiss	Mean of one hour (°C), measured 2 meter above ground	Activity pattern (House et al. 1980, Innes 1996, Kéry et al. 2009, Blanke 2010)
Precipitation	2 mm	Yes	Repeated	Region	MeteoSwiss	Sum over the last 24 hours (mm)	Activity pattern (Kéry et al. 2009)
Sunshine	0.74 h	Yes	Repeated	Region	MeteoSwiss	Sum of minutes (%) over the last one hour (h)	Activity pattern (NCC 1983, Elbling 1997)
Wind speed scalar	7 km/h	Yes	Repeated	Region	MeteoSwiss	Scalar, mean of one hour (km/h)	Activity pattern (Kéry et al. 2009)

TABLE 2. Explanatory variables

Explanatory variables	Mean	Used in analysis	Sampling interval	Spatial reference	Source	Measuring detail	Context / Reference
Slope width	6.0 m	Yes	Once	Site	Measure	Measured at meter 60 of site (m)	Available surface
Exposition	176°	Yes	Once	Site	Measure	Measured on a map (°) (map.bafu.admin.ch)	Thermoregulation (Bischoff 1988, Hofer et al. 2001, Kéry et al. 2009)
Month of first cut	4.4	Yes	Repeated	Site	Observation	More than ¼ of surface was cut the first time before end of month (May = 5, September = 9)	Disturbance, forage, thermoregulation
Mulch	0.3	Yes	Repeated	Site	Observation	The cut plant material was left on site after cutting (mulching) (yes = 1, no = 0)	Disturbance, thermoregulation
Vegetation height	17 cm	Yes	Repeated	Plot	Measure	We let fall a box (material: plastic, size: 335 mm x 390 mm x 170 mm, weight: 620 g) from 1 m height onto the vegetation and measured the distance (cm) between the box and the ground on all 4 sides of the box. For the analysis we took the mean value of the 4 distances. We did not apply the method if the vegetation was higher than 1 m.	Thermoregulation (Podloucky 1988, Gramentz 1996, Märtens et al. 1997)
Litter quantity	2.1	Yes	Once	Plot	Estimate	Mean litter quantity of 5 plots (ordinal: very high = 5, high = 4, medium = 3, low = 2, very low = 1)	Basking spot, shelter structure (Schnürer et al. 2010)
Number of rodent holes	5.5	Yes	Once	Plot	Count	Sum of rodent holes counted on 5 plots	Shelter structure (NCC 1983)

Explanatory variables	Mean	Used in analysis	Sampling interval	Spatial reference	Source	Measuring detail	Context / Reference
Soil sand content	3.2	Yes	Once	Plot	Estimate	Mean tactual estimate of 5 plots (ordinal: sandy soil = 5, loamy sand = 4, sandy loam = 3, loam = 2, clay = 1) (Brunner et al. 2002)	Nesting structure (Rykena and Nettmann 1987, Andrén et al. 1988, Bischoff 1988, Strijbosch 1988, Blanke 2010)
Soil skeleton content	2.5	Yes	Once	Plot	Estimate	Mean tactual and visual estimate of 5 plots (ordinal: very high = 5, high = 4, medium = 3, low = 2, very low = 1) (Brunner et al. 2002)	Nesting structure
Soil humus content	1.8	No, correlated by -0.69 with soil sand content	Once	Plot	Estimate	Mean tactual and visual estimate of 5 plots (ordinal: very high = 5, high = 4, medium = 3, low = 2, very low = 1) (Brunner et al. 2002)	Nesting structure
Cover of herbaceous vegetation	73 %	Yes	Once	20 m- sector	Estimate	Mean ocular estimate (%) of 5 sectors	Thermoregulation (Podloucky 1988, Gramentz 1996, Märtens et al. 1997)
Cover of woody vegetation	4 %	Yes	Once	20m- sector	Estimate	Mean ocular estimate (%) of 5 sectors	Thermoregulation (Bischoff 1988, Podloucky 1988, Krug et al. 1996, Schnürer et al. 2010)
Cover of open ground, such as soil, grid, sand or litter	5 %	Yes	Once	20m- sector	Estimate	Mean ocular estimate (%) of 5 sectors	Thermoregulation (Bischoff 1988, Krug et al. 1996)

Explanatory variables	Mean	Used in analysis	Sampling interval	Spatial reference	Source	Measuring detail	Context / Reference
Cover of solid material, such as cable ducts, concrete constructions, rock surfaces or piles of stones	3 %	Yes	Once	20m- sector	Estimate	Mean ocular estimate (%) of 5 sectors	Basking spot, shelter structure, thermoregulation (House et al. 1980, Blanke 2010, Schnürer et al. 2010)
Cover of gravel	9 %	Yes	Once	20m- sector	Estimate	Mean ocular estimate (%) of 5 sectors	Basking spot, shelter structure, thermoregulation (Bischoff 1988, Krug et al. 1996, Blanke 2010)
Cover of woody structures, such as dead wood, piles of wood or woody railway sleepers	1 %	Yes	Once	20m- sector	Estimate	Mean ocular estimate (%) of 5 sectors	Basking spot, shelter structure, thermoregulation (House et al. 1980, Blanke 2010, Schnürer et al. 2010)
Cover of thorn stands, such as roses or blackberries	5 %	Yes	Once	20m- sector	Estimate	Mean ocular estimate (%) of 5 sectors	Shelter structure (Blanke 2010)
Cover of herbaceous vegetation	81 %	No, correlated by 0.53 with cover of herbaceous vegetation	Once	Plot	Estimate	Mean ocular estimate (%) of 5 plots	Thermoregulation (Podloucky 1988, Gramentz 1996, Märtens et al. 1997)
Cover of open ground, such as soil, litter, grit or sand	12 %	No, correlated by 0.62 with cover of open ground	Once	Plot	Estimate	Mean ocular estimate (%) of 5 plots	Basking spot, shelter structure, thermoregulation (Bischoff 1988, Krug et al. 1996)

Explanatory variables	Mean	Used in analysis	Sampling interval	Spatial reference	Source	Measuring detail	Context / Reference
Cover of gravel and stones	7 %	No, correlated by 0.61 with cover of gravel	Once	Plot	Estimate	Mean ocular estimate (%) of 5 plots	Basking spot, shelter structure, thermoregulation (Bischoff 1988, Krug et al. 1996, Blanke 2010)
Plant species number	11.3	Yes, but correlated by 0.89 with Shannon index, not used in the same models	Once	Plot	Observation	Mean of total number of 5 plots	General habitat indicator
Shannon index	1.7	Yes, but correlated by 0.89 with plant species number and by 0.68 with Shannon equitability, not used in the same models	Once	Plot	Calculation	Calculated by determining for each species the proportion of individuals that it contributes to the total in the sample $H = -\sum_{i=1}^{S} P_i \, lnP_i$ (Begon et al. 2006)	General habitat indicator
Shannon equitability	0.7	Yes, but correlated by 0.68 with Shannon index, not used in the same models	Once	Plot	Calculation	Quantified by Shannon index H, as a proportion of the maximum possible value H would assume if individuals were completely evenly distributed amongst the species $J = \frac{H}{H\,max} = \frac{-\sum_{i=1}^{S} P_i lnP_i}{\ln S}$ (Begon et al. 2006)	General habitat indicator

Explanatory variables	Mean	Used in analysis	Sampling interval	Spatial reference	Source	Measuring detail	Context / Reference
Landolt value for soil moisture F	2.9	Yes, but correlated by -0.7 with L, and by 0.77 with N, not used in the same models	Once	Plot	Calculation	Weighted site averages of 5 plots (ordinal: 1 = very dry, 5 = flooded) (Landolt 1977)	Thermoregulation, general habitat indicator (Märtens 1999, Hofer et al. 2001, Diekmann 2003)
Landolt value for light L	3.4	Yes, but correlated by -0.7 with F, not used in the same models	Once	Plot	Calculation	Weighted site averages of 5 plots (ordinal: 1 = deep shade, 5 = full light) (Landolt 1977)	Thermoregulation, general habitat indicator (Märtens 1999, Hofer et al. 2001, Diekmann 2003)
Landolt value for soil nutrients N	3.4	Yes, but correlated by 0.77 with F, not used in the same models	Once	Plot	Calculation	Weighted site averages of 5 plots (ordinal: 1 = very infertile, 5 = very fertile and over-rich)(Landolt 1977)	General habitat indicator (Märtens 1999, Diekmann 2003)
Adult *P. muralis*	2.5	Yes	Repeated	Site	Count	Maximum value of counted adult individuals	Competition (Hofer et al. 2001)
Cats	0.4	Yes	Repeated	Site	Counts	Total number of observed domestic cats	Predation (Hofer 1998, Blanke 2010)

TABLE 3. List of models used to describe detection probabilities, ranked by their AIC value (explanatory variables set constant, data distribution: negative binominal).

Observation covariables	Number of covariables	Delta AIC	Akaike weight
Observation duration + observation duration^2	5	0.0	0.98
Observation duration	4	7.6	0.02
Sunshine + sunshine^2	5	17.9	0.00
Wind speed	4	20.6	0.00
Sunshine	4	20.8	0.00
Air humidity	4	21.3	0.00
Precipitation	4	21.3	0.00
Solar radiation + solar radiation^2	5	21.4	0.00
Date	4	21.7	0.00
Wind speed + wind speed^2	5	22.1	0.00
Air temperature	4	22.7	0.00
Air humidity + air humidity ^{2}	5	22.7	0.00
Time of day	4	23.0	0.00
Solar radiation	4	23.1	0.00
Date + date^2	5	23.3	0.00
Precipitation + precipitation^2	5	23.3	0.00
Time of day + time of day ^{2}	5	24.6	0.00
Air temperature + air temperature^2	5	24.7	0.00

TABLE 4. Composition of candidate models for estimation of site specific abundance

Model	Explanation	Explanatory variables
1	The availability of structures used as basking spots influence the abundance of *L. agilis*	Exposition + exposition^2 + litter quantity + litter quantity^2 + cover of solid material + cover of solid material^2 + cover of gravel + cover of woody structures + Landolt value for light + Landolt value for light^2
2	The predation through cats in combination with competition with *P. muralis* and the availability of shelter structures influence the abundance of *L. agilis*	Cats + litter quantity + litter quantity^2 + rodent holes + rodent holes^2 + cover of solid material + cover of solid material^2 + cover of gravel + cover of woody structures + cover of thorn stands + adult *P. muralis*
3	The availability of woody structures which have a high heat storage capacity, the received quantity of light and Landolt values which indicate a dry microclimate influence the abundance of *L. agilis*	Exposition + exposition^2 + litter quantity + litter quantity^2 + cover of woody structures + Landolt value for light + Landolt value for light^2
4	The availability of areas without vegetation cover influences the abundance of *L. agilis*	Litter quantity + litter quantity^2 + cover of herbaceous vegetation + cover of herbaceous vegetation^2 + cover of open ground + cover of gravel + Landolt value for light + Landolt value for light^2
5	The predation through cats and the availability of shelter structures influence the abundance of *L. agilis*	Cats + litter quantity + litter quantity^2 + rodent holes + rodent holes^2 + cover of solid material + cover of solid material^2 + cover of gravel + cover of woody structures + cover of thorn stands
6	The predation through cats influences the abundance of *L. agilis*	Cats
7	The exposition and the width of the slope influence the abundance of *L. agilis*	Slope width + slope width^2 + exposition + exposition^2
8	The competition with *P. muralis* influences the abundance of *L. agilis*	Adult *P. muralis*
9	The availability of different habitat structures influences the abundance of *L. agilis*	Vegetation height + litter quantity + litter quantity^2 + rodent holes + rodent holes^2 + cover of woody vegetation + cover of woody vegetation^2+ cover of open ground + cover of solid material + cover of solid material^2+ cover of gravel + cover of woody structures + cover of thorn stands + plant species number + Shannon index
10	The availability of structures used as shelter influence the abundance of *L. agilis*	Litter quantity + litter quantity^2 + rodent holes + rodent holes^2 + cover of woody vegetation + cover of woody vegetation^2 + cover of solid material + cover of solid material^2 + cover of woody structures + cover of thorn stands

Model	Explanation	Explanatory variables
11	The number of plant species and their Shannon index influence the abundance of *L. agilis*	Plant species number + Shannon index
12	The Landolt values of the vegetation influence the abundance of *L. agilis*	Landolt value for soil moisture + Landolt value for light + Landolt value for soil nutrients
13	The management regime influences the abundance of *L. agilis*	Month of first cut + month of first cut^2 + vegetation height + litter quantity + litter quantity^2 + cover of thorn stands
14	The availability of stony structures which have a high heat storage capacity, the received quantity of light and Landolt values which indicate a dry microclimate influence the abundance of *L. agilis*	Exposition + exposition^2 + soil sand content + cover of solid material + cover of solid material^2 + cover of gravel + Landolt value for light + Landolt value for light^2
15	Soil parameters influence the abundance of *L. agilis*	Rodent holes + rodent holes^2 + soil sand content + soil skeleton content + Landolt value for soil moisture + Landolt value for soil moisture^2
16	The structure of the vegetation and species richness influence the abundance of *L. agilis*	Vegetation height + cover of herbaceous vegetation + cover of herbaceous vegetation^2 + cover of woody vegetation + cover of woody vegetation^2+ Shannon equitability + Shannon equitability^2 + Landolt value for soil nutrients + Landolt value for soil nutrients^2

TABLE 5. Results of the model selection to estimate site specific abundance, models are ranked by their AIC value (details of models are shown in Table 4 for the candidate models and in Table 6 for the stepwise best ranked model, data distribution stepwise model: zero inflated Poisson, data distribution candidate models: negative binomial)

Model	Number of explanatory variables	Delta AIC	Akaike weight
stepwise	30	0.0	1.00
1	15	34.0	0.00
2	16	39.9	0.00
3	12	40.9	0.00
4	13	41.6	0.00
5	15	43.0	0.00
6	6	43.2	0.00
7	9	43.2	0.00
8	6	44.1	0.00
9	20	44.6	0.00
10	15	45.5	0.00
11	7	46.1	0.00
12	8	46.7	0.00
13	12	47.4	0.00
14	13	47.5	0.00
15	11	49.9	0.00
16	14	50.9	0.00

TABLE 6. Details of the stepwise best ranked model (data distribution: zero inflated Poisson)

Observation covariables	Estimates	95% Confidence interval		Change in AIC, with/without covariable	p- value
Intercept	-1.72	-2.05	-1.39		< 0.001
Observation duration	0.48	0.30	0.67	22.8	< 0.001
Observation duration^2	-0.18	-0.28	-0.07	9.5	0.001

Explanatory variables	Estimates	95% Confidence intervals		Change in AIC, with/without variable	p- value
Intercept	4.66	3.78	5.54		< 0.001
Slope width	-1.12	-1.55	-0.70	29.3	< 0.001
Slope width^2	0.38	0.22	0.54	21.2	< 0.001
Exposition	0.38	0.12	0.63	38.9	0.004
Exposition^2	-0.70	-0.94	-0.45	34.3	< 0.001
Month of first cut	-0.51	-0.77	-0.24	30.2	< 0.001
Month of first cut^2	-1.95	-2.64	-1.26	32.1	< 0.001
Mulch				1.6	
Mulch^2				3.6	
Vegetation height	0.62	0.22	1.01	7.8	0.002
Vegetation height^2				0.9	
Litter quantity	-0.18	-0.47	0.11	46.0	0.228
Litter quantity^2	-0.39	-0.63	-0.14	11.5	0.002
Rodent holes	0.77	0.44	1.10	21.6	< 0.001
Rodent holes^2	-0.25	-0.37	-0.12	13.9	< 0.001
Soil sand content	0.57	0.29	0.84	16.2	< 0.001
Soil sand content^2				1.8	
Soil skeleton content				0.4	
Soil skeleton content^2				2.4	
Cover of herbaceous vegetation	0.18	-0.74	1.10	23.0	0.707
Cover of herbaceous vegetation^2	0.65	0.37	0.92	21.7	< 0.001
Cover of woody vegetation	0.36	-0.43	1.14	5.5	0.373
Cover of woody vegetation^2	-0.25	-0.44	-0.06	4.5	0.010
Cover of open ground	-0.29	-0.68	0.09	0.2	0.136
Cover of open ground^2				2.0	
Cover of solid material				1.8	
Cover of solid material^2				3.8	
Cover of gravel	-1.41	-2.21	-0.61	11.4	< 0.001
Cover of gravel^2	0.42	0.17	0.66	9.2	< 0.001
Cover of woody structures	0.43	0.16	0.69	8.3	0.002
Cover of woody structures^2				1.7	
Cover of thorn stands	-1.48	-2.42	-0.53	7.8	0.002
Cover of thorn stands^2				1.7	
Plant species number				1.4	
Plant species number^2				3.4	
Shannon index				1.3	

Explanatory variables	Estimates	95% Confidence intervals	Change in AIC, with/without variable	p- value	Explanatory variables
Shannon index^2				3.2	
Shannon equitability	-0.21	-0.48	0.06	25.0	0.131
Shannon equitability^2	-0.61	-0.87	-0.36	33.0	< 0.001
Landolt value for soil moisture				2.0	
Landolt value for soil moisture^2				2.8	
Landolt value for light	-0.44	-0.79	-0.08	11.9	0.015
Landolt value for light^2	0.24	0.07	0.42	5.5	0.006
Landolt value for soil nutrients				0.9	
Landolt value for soil nutrients^2				2.8	
Adult *P. muralis*				2.0	
Adult *P. muralis* ^{2}				3.3	
Cats				1.9	
Cats^2				3.6	

Figures

FIGURE 1. Effect of observation duration on the expected detection probability of *L. agilis* (black line), based on prediction of model 15. Grey lines are 95% confidence intervals.

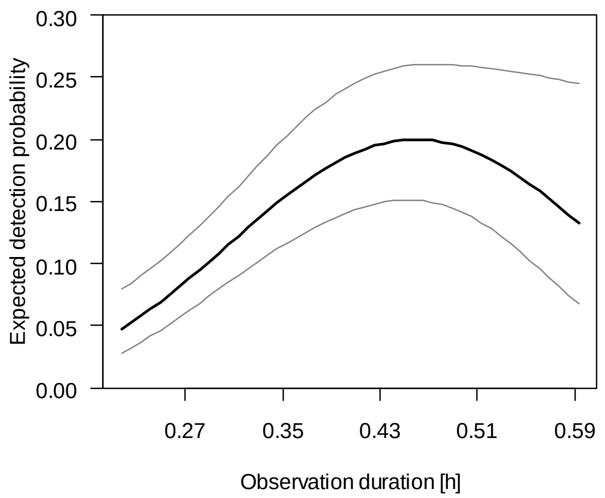
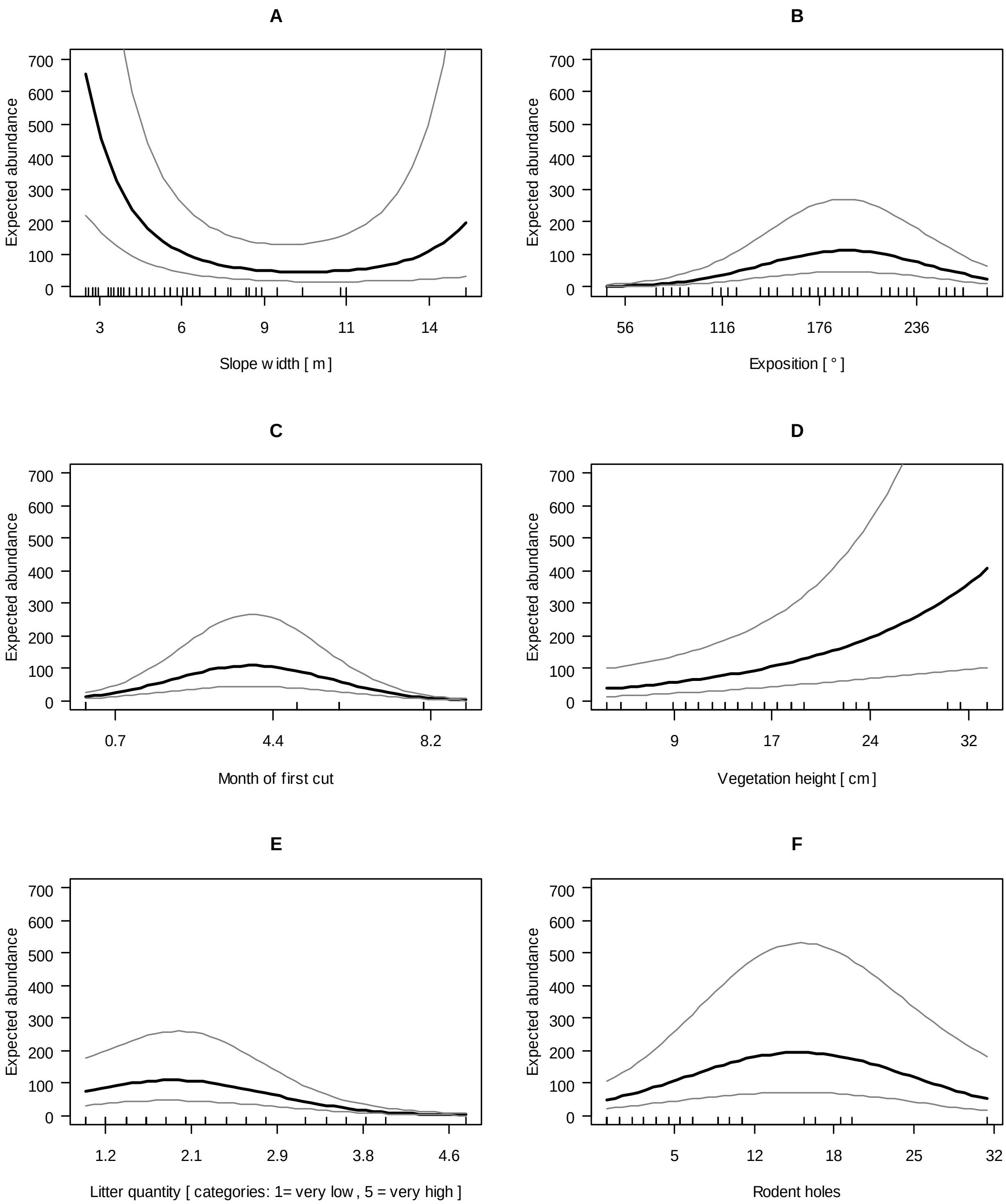
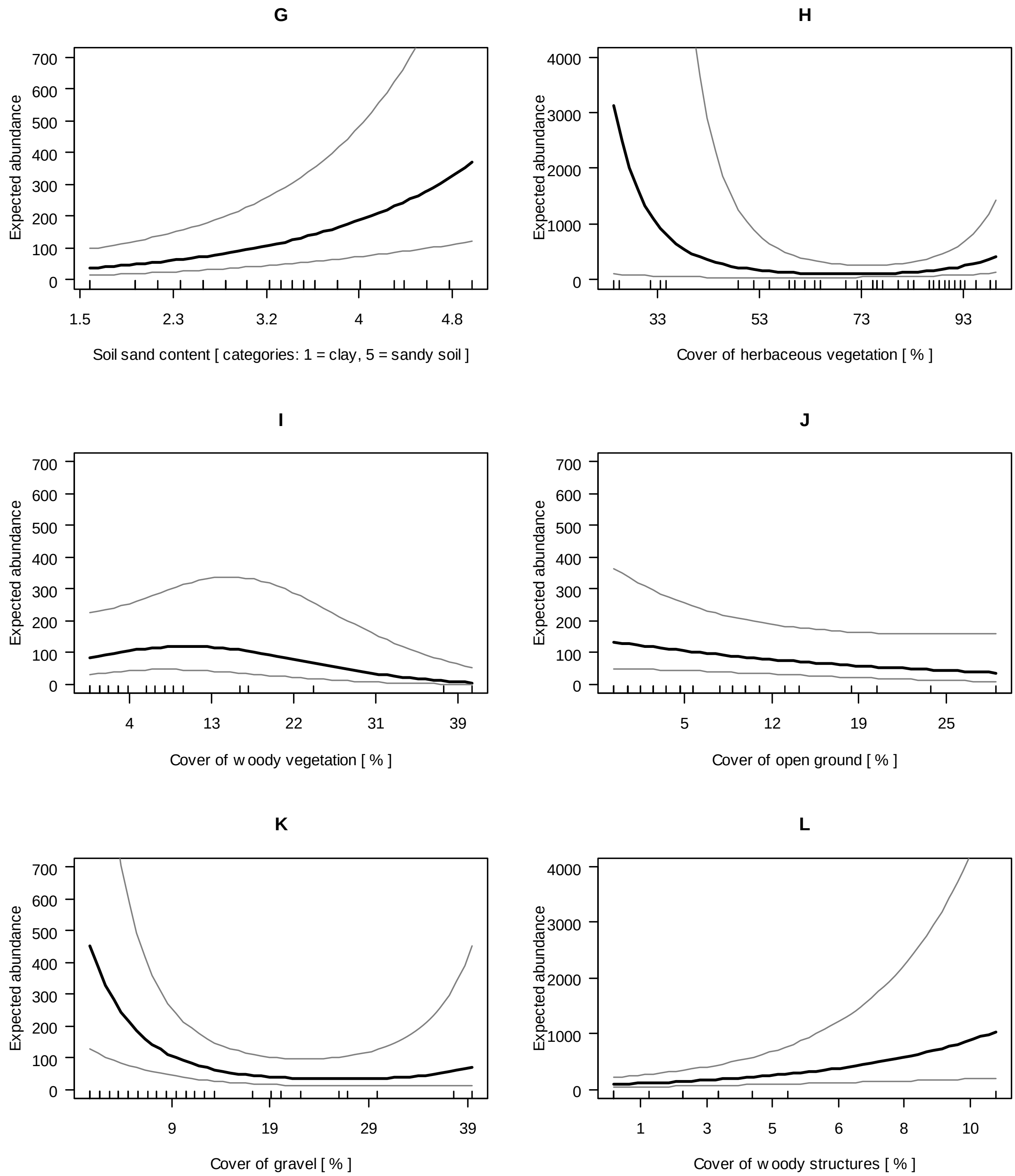
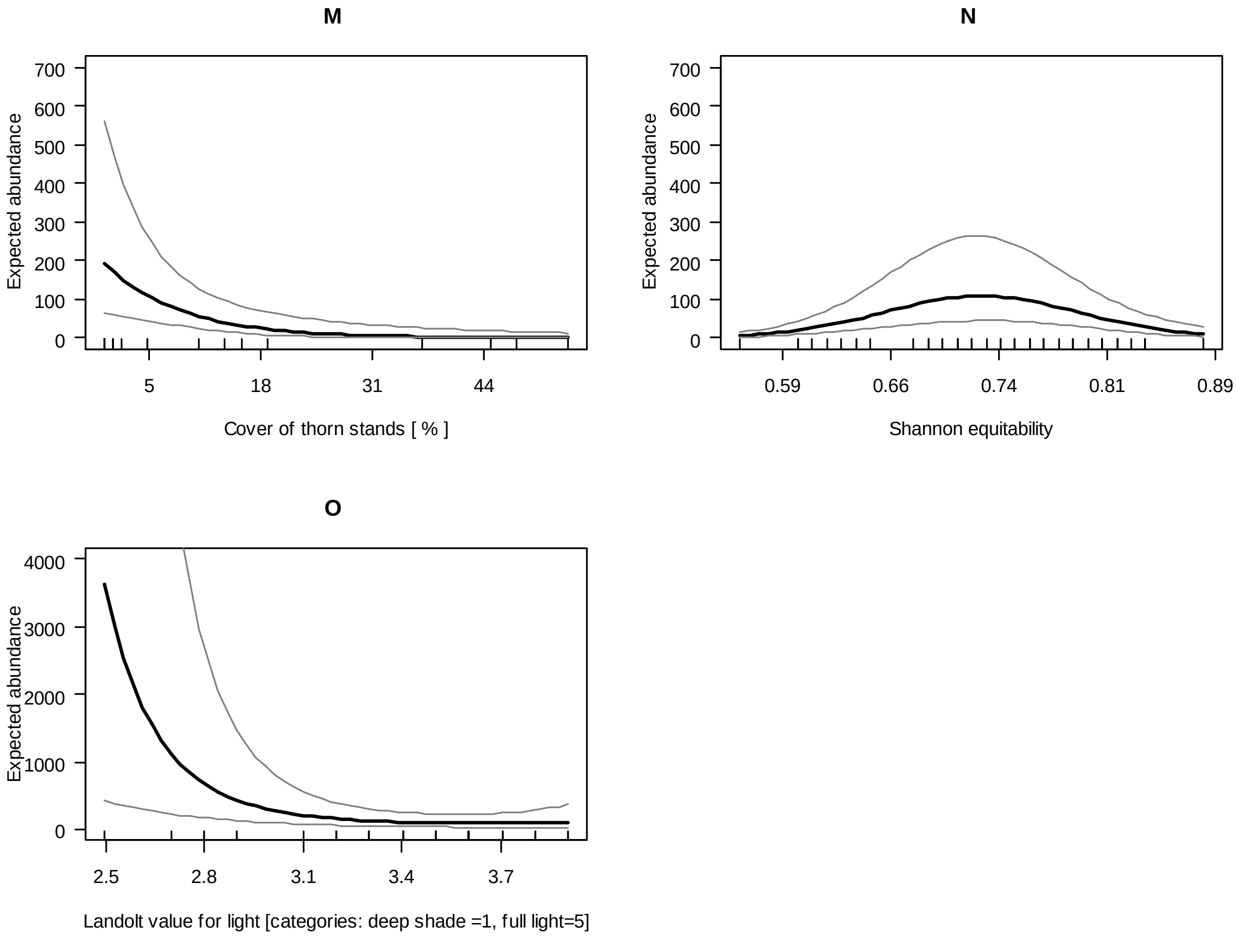


FIGURE 2. Relationship between expected abundance of *L. agilis* and explanatory variables (black line), based on predictions of model 15 (all other than the plotted explanatory variables were set to the mean). Uncertainty intervals are 95% confidence intervals (grey line). Note that the scale of the y- axis ranges either up to 700 or up to 4000.


A
B
C
D
E
F
Expected abundance
0
100
200
300
400
500
600
700
3
6
9
11
14
Slope w idth [m]
56
116
176
236
Exposition [°]
0.7
4.4
8.2
Month of first cut
9
17
24
32
Vegetation height [cm]
1.2
2.1
2.9
3.8
4.6
Litter quantity [categories: 1= very low , 5 = very high]
5
12
18
25
32
Rodent holes


G
Expected abundance
0
100
200
300
400
500
600
700
1.5
2.3
3.2
4
4.8
Soil sand content [categories: 1 = clay, 5 = sandy soil]
H
Expected abundance
0
1000
2000
3000
4000
33
53
73
93
Cover of herbaceous vegetation [%]
I
Expected abundance
0
100
200
300
400
500
600
700
4
13
22
31
39
Cover of w oody vegetation [%]
J
Expected abundance
0
100
200
300
400
500
600
700
5
12
19
25
Cover of open ground [%]
K
Expected abundance
0
100
200
300
400
500
600
700
9
19
29
39
Cover of gravel [%]
L
Expected abundance
0
1000
2000
3000
4000
1
3
5
6
8
10
Cover of w oody structures [%]


M
N
O
Expected abundance
700
600
500
400
300
200
100
0
5
18
31
44
Cover of thorn stands [%]
0.59
0.66
0.74
0.81
0.89
Shannon equitability
4000
3000
2000
1000
2.5
2.8
3.1
3.4
3.7
Landolt value for light [categories: deep shade =1, full light=5]

Erklärung

gemäss Art 28. Abs. 2 RSL 05

Name / Vorname:	Stoll Simona
Matrikelnummer:	04-869-574
Studiengang:	Ecology and Evolution
Abschluss:	Masterarbeit
Titel der Arbeit:	How site characteristics, competition and predation influence site specific abundance of sand lizard on railway banks
Leiter der Arbeit:	Prof. Dr. Markus Fischer Institut für Pflanzenwissenschaften, Botanischer Garten und Oeschger Zentrum, Universität Bern und Dr. Benedikt R. Schmidt Koordinationsstelle für Amphibien- und Reptilienschutz in der Schweiz und Institut für Evolutionsbiologie und Umweltwissenschaften, Universität Zürich

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Bern, 05.07.2013 Simona Stoll