SALAMANDRA **49**(2) | 97–104 | 30 June 2013 | ISSN 0036–3375

Do introduced wall lizards (*Podarcis muralis*) cause niche shifts in a native sand lizard (*Lacerta agilis*) population? A case study from south-western Germany

Aurelius Heym [1], Guntram Deichsel [2], Axel Hochkirch [1], Michael Veith [1]
& Ulrich Schulte [1]

[1] Universität Trier, Biogeographie, Fachbereich VI, Universitätsring 15, 54296 Trier, Germany
[2] Friedrich-Ebert-Str. 62, 88400 Biberach an der Riss, Germany

Corresponding author: Ulrich Schulte, e-mail: schulte@uni-trier.de

Manuscript received: 22 January 2013

Abstract. Numerous introductions of common wall lizards (*Podarcis muralis*) into populations of native sand lizards (*Lacerta agilis*) are known from Germany. Since the sand lizard is strongly protected by national and European laws, it is crucial to evaluate the potential for a competitive displacement of sand lizards by alien wall lizards. We here studied for the first time the impact of introduced *P. muralis* on native sand lizards. We compared spatial distribution, micro-habitat choice, behavioural thermoregulation, activity patterns and interactions of *L. agilis* in Nürtingen, Germany, in the presence and absence of introduced wall lizards originating from northern Italy. Our results show that the spatial distribution of both species and their local dispersal was strongly overlapping. The overlap in substrate selection between both species was significantly higher than expected (86%), with the strongest niche overlap between males of both species. Within the syntopic population, the population size of *L. agilis* was estimated at 69 ± 7 individuals, whereas the population size of *P. muralis* was estimated at ca. 192 individuals. Dorsal temperature of *P. muralis* was on average 2°C higher than the ambient air temperature (indicating a very effective thermoregulation), whereas dorsal temperature of *L. agilis* corresponded approximately with ambient air temperatures on both study sites. While *P. muralis* showed intraspecific interactions more often, interspecific interactions were rare (mainly basking at a distance). We did not detect any shift in habitat use or thermoregulation of sand lizards in the presence of introduced wall lizards. However, the strong niche overlap between both species in syntopy calls for further studies on their interspecific competition, both *in situ* (e.g., during the spring season) and experimentally.

Key words. Squamata, Lacertidae, *Lacerta agilis, Podarcis muralis,* invasive species, microhabitat, thermoregulation, interspecific competition.

Introduction

In south-western Germany, sand and wall lizards (*Lacerta agilis* and *Podarcis muralis*) are naturally found in syntopy only rarely. In the few syntopic populations, e.g., around dry stone wall habitats, both species show a pronounced microhabitat partitioning (Waitzmann 1989, Zimmermann 1989). While the vertical parts of walls are inhabited by *Podarcis muralis*, *Lacerta agilis* usually lives in the ground vegetation stratum (see also Fritz 1987). However, in addition to natural wall lizard populations, there is also an increasing number of records of introduced populations from southern Europe which might differ in ecology. A total of 93 introduced wall lizard populations are currently known from Germany, which stem from eight different genetic lineages (Schulte et al. 2012a). Many of these populations have been established for 15–140 years and are still expanding. While most of these populations have established themselves outside the native range of the species, introductions of non-native lineages along the Upper Rhine Rift represent a serious threat to the genetic integrity of native populations due to the rapid creation of hybrid swarms (Schulte et al. 2012c). Although at least 25 of these locations are known as sand lizard habitats, competition between introduced wall lizards and native sand lizard populations has not been studied and reported to-date only anecdotically (Münch 2001, Steinicke 2000, Schulte et al. 2008, Schulte 2009). Information on competition between invasive wall lizard populations and other native lizards is available from the UK and North America. Mole (2008) studied the impacts of introduced wall and green lizards (*Lacerta bilineata*) on native common lizards (*Zootoca vivipara*) in Dorset, England. He found an increase of 40% in population size of introduced wall lizards and a decrease of 75% in the common lizard population between 2002 and 2007. However, this author argued that these contrasting population trends might not only be explained by competition, but also by insufficient conservation management and changing climatic conditions. In laboratory experiments, Bertram (2004) and Allan et al. (2006) detected an avoidance response of the northern alligator lizard (*Elgaria coerulea*), native to Canada, when exposed to scent marks of introduced wall lizards. Similar observations have been made within an introduced syntopic population of *P. muralis* and *P. liolepis* in Lower Saxony (Schulte et al. 2012b).

We here studied the spatial distribution and habitat selection (microhabitats) of sand lizard populations in the presence or absence of introduced wall lizards. We tested the hypothesis that in syntopy, both species compete in their habitat choice. We analysed substrate selection, dorsal temperature relative to ambient temperature, and spatial distribution of the sand lizard in a pure and a mixed population. Finally, direct interactions between the sand and wall lizards were analysed in more detail to test the assumption that wall lizards would behave aggressively and territorially toward sand lizards.

Material and methods

The study sites

The study was carried out in 2011, in the reproductive and hatching period (between 22 June and 30 August), in two natural populations *L. agilis* near Nürtingen (WSG84: 48°37'36" N, 09°20'07" E), Baden-Württemberg. On one study site (Tiefenbachtal, Fig. 1), a non-native wall lizard population had been discovered by Gabriel Werner in March 2010, which stems from an introduction of eleven specimens from Lake Garda in northern Italy in 1990 (Southern Alps lineage, *Podarcis muralis maculiventris*-West). The initial release site is situated in a traditional orchard, which is inhabited by sand lizards. This locality represents a typical sand lizard habitat without stony substrate and without wall or rock structures, which are typical of native wall lizard habitats. In contrast to natural wall lizard populations in Germany, the introduced wall lizards inhabit slopes with numerous rodent holes at this site, a microhabitat usually utilized by *L. agilis* (Blanke 2010). Although these slopes and a paved path that crosses the orchard represent the only thermal reservoir (e.g., for basking), this population has established itself successfully during the last 20 years. As a control group, we studied a nearby pure population of *L. agilis* in a well-structured private garden property surrounded by orchards in Frickenhausen (Fig. 2) (ten surveys), two kilometres south of the site "Tiefenbachtal" (26 surveys).

Field studies and data analysis

The dorsal colour pattern of all observed sand lizard individuals was photographed for individual recognition (Märtens & Grosse 1996, Blanke 2010). We abstained from recording individual recognition characters of wall lizards due to their large population density and since this method is impossible to effect without capture and disturbance (Schmidt-Loske 1996). Due to the bimodal activity period of both species during the summer months, the study sites were surveyed from 8:30 to 13:00 and from 17:00 to 20:00 (Schulte 2008, Blanke 2010). The sites were visited in an alternate order. Each lizard sighting (Tiefenbachtal: *L. agilis*, n = 257; *P. muralis*, n = 102) was recorded with a GPS (Garmin GPS 12). Behavioural observations were made for 30 minutes per individual. Weather condition, sex, age, Picture ID and extent of autotomy were documented for each observation and specimen. Within this period of 30 minutes, we recorded every five minutes the exact locality, exposure, dorsal lizard temperature, vegetation cover (estimated in %), behaviour, and inter- or intraspecific interactions. The following types of behaviour were distinguished: basking, escape, feeding, exploring,

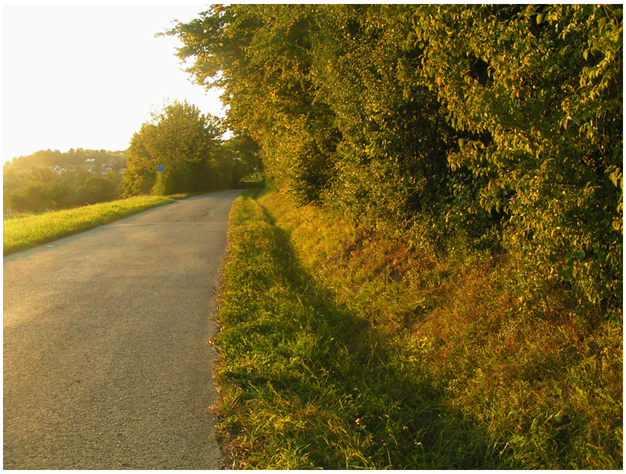

Figure 1. Study site Tiefenbachtal, where *L. agilis* and introduced *P. muralis* occur.

Figure 2. Study site Frickenhausen.

foot shaking, chasing away, hiding, is chased away, lambency, change of location, fighting and hunting (Font et al. 2012). In total, we made 55 observations in the Tiefenbachtal (*L. agilis*, n = 28; *P. muralis*, n = 27) and 25 sand lizard observations in Frickenhausen.

We analysed recapture rates for female and male sand lizards at Tiefenbachtal and Frickenhausen using the POPAN model as incorporated in MARK (White & Burnham 1999). For each data set we tested if the complete model matched the data better than models with constant, temporally varying or sexually discriminating parameters. We used the sinus or logit functions for survival (φ) and detection probabilities (p). We always used the Mlogit link function for the probability of entry (pent) and the log-link function for N (as recommended by Schwarz & Arnason 2007). The best-fitting model was chosen using the Akaike Information Criterion (AICc; Burnham & Anderson 2002). Since the wall lizards at Tiefenbachtal were not individually recognised, we counted all adult individuals by slowly walking through the entire habitat. Subsequently, we adjusted these counts for specimens not recorded by multiplying them with a correction factor of four as recommended by Laufer (1998).

We calculated mobility parameters for nine sand lizards (5 females, 4 males) that were recaptured three to fourteen times in Tiefenbachtal (26 surveys) and for five sand lizards that were recaptured three to eight times in Frickenhausen (10 surveys) using the packages "animal movement" and "homerange analysis" for ArcGIS 3.2. The first capture locality was supposed to be within an individual's home range and used as the home reference position. Since recapture events were limited and below 30 points, it was not possible to calculate Kernel Home Ranges. Therefore, it is likely that our home range estimates using Minimum Convex Polygons do not represent the complete home range of individuals (Rose 1982). We calculated the dispersal (the Morisita index, Iσ) for both species to analyse their spatial distribution. In general, the spatial distribution of a species can be random, uniform or clumped. The Morisita index was developed to test the influence of grid square size on the degree of aggregation (Morisita 1959). For the calculation of Iσ we first calculated grids for both study sites in ArcGIS with three different square sizes (25, 100 and 400 m^2). The distribution is random when Iσ = 1, uniform when Iσ < 1 and clumped if Iσ > 1. Statistical significance of the Morisita index was tested with a Chi^2-Test in R 2.14.0 (R Core Team 2012). Substrate or ground level temperature was recorded as the available environmental temperature with temperature data loggers (Tiny Tag plus by Gemini) at the basking sites of lizards every ten minutes for the whole study period. In addition, we measured the dorsal temperatures of lizards with an infrared thermometer (Peaktech, model: 4990) from a distance of ca. 1.5 m. We tested for differences between dorsal and substrate temperatures of lizards at the same time with a paired t-test in R 2.14.0.

We analysed niche overlap between sand lizards in Tiefenbachtal and Frickenhausen and between sand and wall lizards in Tiefenbachtal with respect to substrate choice in EcoSim 7.0 (Gotelli & Entsminger 2004). We applied the Czechanowski index, which ranges from 0 (no shared resources) to 1 (identical habitat utilization). We weighted the different substrates according to their observed availability on both study sites as follows: 1. Tiefenbachtal: bare ground 15%, stones 1%, woody debris 5% and vegetation 79%. 2. Frickenhausen: bare ground 10%, stones 5%, woody debris 7% and vegetation 78%. To test if the observed niche overlap differed from a random pattern, we carried out a null-model analysis as incorporated in EcoSim 7.0 (Gotelli & Entsminger 2004). EcoSim simulates patterns of niche overlap and compares these randomised results with the observed data matrix. We used the algorithm RA3 (Winemiller & Pianka 1990) to test for non-random niche overlap. This procedure retains the observed niche breadth of each species, yet allows the utilization of any resource state, including categories that were available but not used by the species. For each data set, 10,000 replicates were run in the simulation.

Results

Population sizes and mobility

We recorded a total of 44 adult sand lizards in the syntopic population (Tiefenbachtal), twenty of which were observed at least two times (recapture rate: 46%) and 16 individuals multiple times. The recapture rate in females was low, but 11 individuals were recaptured at least once (recapture rate: 85%) and 69% were observed multiple times. Similar to the Tiefenbachtal population, the recapture rate was higher in females (88%) than in males (75%). The mean home range size of nine sand lizards that were recaptured at an average of 5.2 times in the Tiefenbachtal was 13.6 m^2 (range: 2–39 m^2), whereas the mean home range size of five sand lizards that were recaptured at least three times in Frickenhausen was substantially larger with 348 m^2 (range: 22–1107 m^2). Mean cumulative distances of 12 recaptured individuals in the Tiefenbachtal were 32 m (range: 5–166 m, SD: ± 44 m, maximum distance: 73 m), whereas for six individuals in Frickenhausen, the mean cumulative distances was 82 m (range: 21–174 m, SD: ± 74 m, maximum distance: 65 m.) The spatial distribution of sand lizard home ranges strongly overlapped with wall lizard occurrences (regardless of the sex).

At both study sites, the best-fitting models for sand lizard population estimation had a time-constant probability of individual entry into the population. We selected the model {phi(.)p(g+t)pent(g·t)N(g)} for the Tiefenbachtal population, whereas the model {phi(.g)p(g·t)pent(g·t) N(g)} fitted best for the Frickenhausen lizards. Under the assumption of constant capture probabilities over time, POPAN estimated the population size at Tiefenbachtal to be 69 ± 7 SE (95% credible interval: 55–83). For Frickenhausen, the population size was estimated to be 13 ± 0.5 individuals (95% credible interval: 12–14). The population size of wall lizards in the Tiefenbachtal was estimated to be 192 individuals.

Spatial distribution and dispersion index

The calculation of the dispersion index Iσ fitted best when both study sites were subdivided into 100 m^2 squares. The spatial distributions of *L. agilis* and *P. muralis* in the Tiefenbachtal were significantly clumped with very high Iσ values (*L. agilis*: Iσ = 21.3, Fig. 3). The spatial overlap of the distributions of both species was significantly larger than expected with a 43.2% overlap (Fisher's Exact Test, p = 0.017). Agglomerations were concentrated in certain habitat structures, such as wooden debris, stone piles and fruit trees. The distribution of *L. agilis* in Frickenhausen was more uniform and only significantly clumped when 100 m^2 squares were considered (Iσ = 2.07, Fisher's Exact Test, p = 0.028).

Niche overlap in microhabitat choice

We found no significant overlap (53.7%) in substrate utilization of allotopic and syntopic sand lizards. To the contrary, niche overlap between syntopic populations of sand lizards and introduced wall lizards in the Tiefenbachtal (86.1%) was significantly larger than expected by chance, demonstrating that both species share the same microhabitat (Table 1). Niche overlap (and therefore the probability of individual encounters) was strongest between males of both species (92%), whereas it was much lower between females (52%). Niche overlap of male sand lizards (69%) in the Tiefenbachtal and Frickenhausen was slightly larger than between females of the same species (62%).

Thermoregulation

Dorsal temperatures and ground temperatures were measured simultaneously for each individual. The mean dorsal temperature of *P. muralis* in the Tiefenbachtal was significantly higher (29.5°C ± 5.8°C, n = 24) than in *L. agilis* (25.6°C ± 4.2°C, n = 28). No significant differences between dorsal temperatures of sand lizards in the presence or absence of introduced wall lizards was found (Tiefenbachtal: 25.6°C ± 4.2°C, n = 28; Frickenhausen 26.2°C ± 4.1°C, n = 25, one-sided t-Test, df = 49, p = 0.240). Compared to the ground temperature (logger), the dorsal temperature of wall lizards was significantly higher by 2°C (Tiefenbachtal: t = -2.47, df = 23, p = 0.021), whereas dorsal temperature of sand lizards differed not significantly from the ground temperature at both study sites (Frickenhausen: paired t-Test: t = -0.33, df = 24, p = 0.742; Tiefenbachtal: t = 1.03, df = 27, p = 0.312).

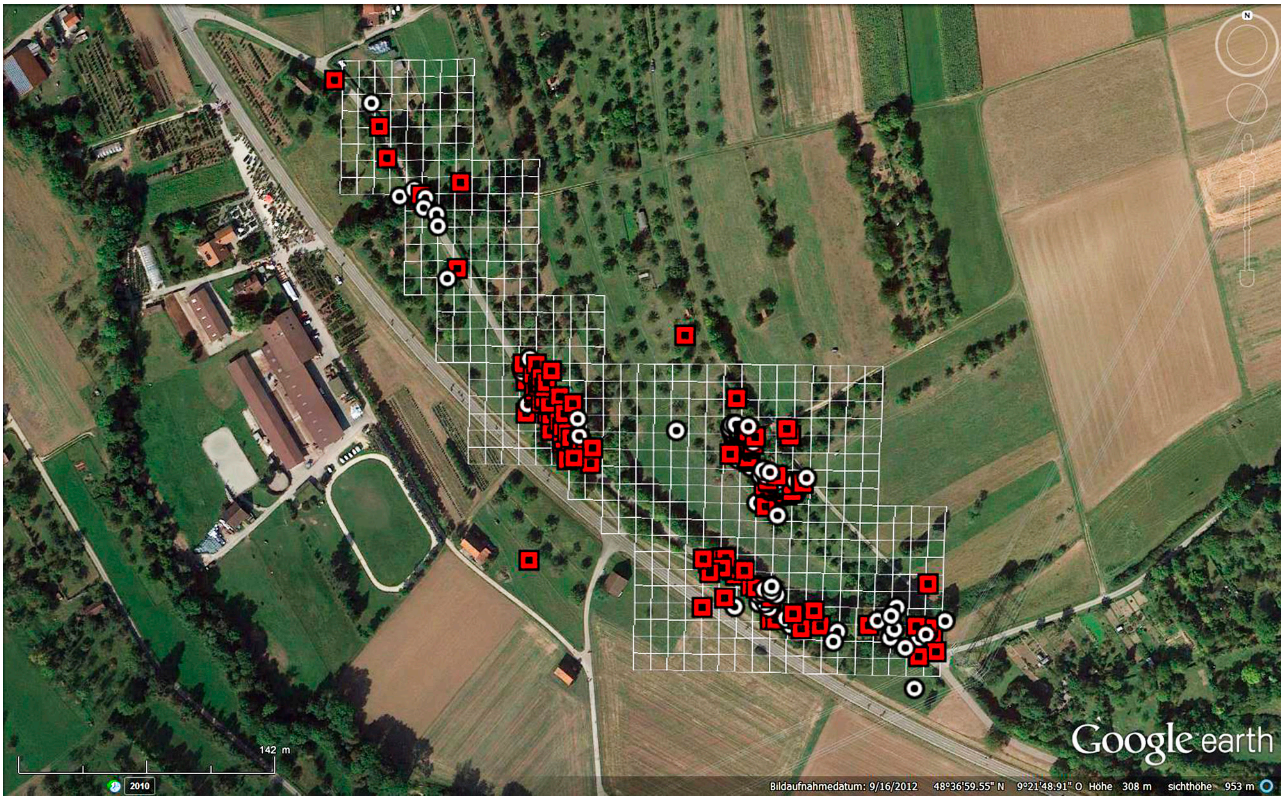

Figure 3. Spatial distribution of sand lizards (red dots) and wall lizards (white dots) at the Tiefenbachtal study site. The 10 × 10 m grid illustrates the area used for the calculation of dispersal indices.

Table 1. Niche overlap with regard to substrate choice between *L. agilis* (LA) and *P. muralis* (PM) in the Tiefenbachtal (TI) and for *L. agilis* in Frickenhausen (FI) calculated with EcoSim 7.0. Asterisk *: significantly larger than expected, ^{ns}: not significant.

	LA ♀ (FR)	PM ♂ (TI)	PM ♀ (TI)	LA ♂ (TI)	LA ♀ (TI)
LA ♂ (FR)	0.61^{ns}	0.7*	0.86*	0.69*	0.5 ^{ns}
LA ♀ (FR)		0.5 ^{ns}	0.59 ^{ns}	0.45 ^{ns}	0.62 ^{ns}
PM ♂ (TI)			0.82*	0.92*	0.56 ^{ns}
PM ♀ (TI)				0.77 ^{ns}	0.52 ^{ns}
LA ♂ (TI)					0.55 ^{ns}

Behavioural patterns

Table 2 shows the observed frequencies as percentages of individual activities of sand lizards and common wall lizards at both sites. Wall lizards spent less time for basking than sand lizards and showed changes in behaviour more frequently. Moreover, common wall lizards were shyer and fled more often. Both species were rarely or never observed hunting or feeding in the Tiefenbachtal, whereas this was frequently observed in sand lizards at Frickenhausen.

Table 2. Behavioural patterns as percentages of sand lizards and wall lizards (TI = Tiefenbachtal, FR = Frickenhausen). Temporal significant activities are highlighted in grey.

	P. muralis	*L. agilis* (TI)	*L. agilis* (FR)
basking	68.84	84.47	82.61
escape	10.01	6.31	3.08
feeding	0.6	/	5.82
exploring	3.57	1.19	/
foot-shaking	5.95	/	/
chasing away	0.89	0.6	/
hiding	0.79	0.36	/
is chased away	1.31	0.6	/
lambency	/	0.69	/
change of location	1.19	/	/
fighting	0.6	/	/
hunting	1.19	3.73	8.48

Inter- and intraspecific interactions

Only four interspecific encounters were observed during the study period. Furthermore two intraspecific interactions of sand lizards and nine intraspecific interactions of wall lizards were observed. Two of the interspecific interactions were "basking at a distance" (5 to 20 cm, Fig. 4). In one case, a male wall lizard chased away a female sand lizard from an open sunny slope. Shortly after this observation, the same but reciprocal behaviour occurred. In another situation, a female sand lizard and a male wall lizard were hiding in the same rodent hole (with body contact). In wall lizards, antagonistic intraspecific behaviour was observed more frequently than in sand lizards.

Discussion

Niche overlap of sand lizards and wall lizards

Our results demonstrate that both lizard species have a clumped dispersal, with a strong overlap in the syntopic population (Tiefenbachtal). Most likely, this dispersal is the result of a limited availability of suitable basking sites for behavioural thermoregulation, such as wood or stones. Indeed, a closer look at the resource "basking site" shows a strong overlap in substrate utilization, which was significantly larger than expected. This means that sand lizards and introduced wall lizards are very similar in their use of places for basking and hiding (Fig. 2). The estimated population size of the common wall lizard (192 individuals) was 2.8 times higher than the calculated population size of the sand lizard (69), however, the difference in approach for estimating population sizes in both species has to be taken into consideration. The higher abundance of wall lizards and the species' territoriality (Weber 1957, Schulte 2008) contribute to a stronger clustering in the occurrence of the species within the syntopic population. All polygons of home ranges of sand lizards included numerous wall lizard sightings, illustrating the strong overlap in the spatial distribution of both species where they live in syntopy.

Analyses of substrate utilization and dorsal temperatures revealed that *P. muralis* attains higher body temperatures from basking more exposed on wooden or rocky substrates, while *L. agilis* was also frequently encountered in the vegetation. Comparing the thermoregulatory and behavioural patterns of both species, wall lizards appear to bask for shorter periods at a time and are more effective than sand lizards. They reached higher dorsal temperatures, constantly above the ambient temperature, whereas the dorsal temperatures of sand lizards corresponded approximately to the ambient temperature. We hypothesize that the smaller body size, mass and more flattened body shape of *P. muralis* allows the species to heat up more rapidly and as a consequence, to display different behaviours (e.g., hunting, Avery 1978) earlier and with greater flexibility than the sand lizard. Moreover, the bimodal activity cycle was less pronounced in wall lizards than in sand lizards. Thus, wall lizards were still active around noon on warm and sunny days when no sand lizard was seen.

Figure 4. Basking at a distance of male sand and wall lizards.

Microhabitat selection of sand lizards in the presence and absence of introduced wall lizards

The question whether habitat selection and spatial distribution of sand lizards differ according to the presence or absence of introduced wall lizards cannot be answered conclusively. The overlap of substrate selection in sand and wall lizards in the Tiefenbachtal was significantly higher than expected. However, we did not detect any shift in microhabitat selection of sand lizards compared to the allotopic population in Frickenhausen. Furthermore, thermoregulatory and behavioural patterns of sand lizards differed not significantly between allotopic and syntopic populations. Therefore, we could not find any evidence of a negative influence of common wall lizards on sand lizards. In the Tiefenbachtal, sand lizards showed a higher degree of aggregation than at Frickenhausen. This strong aggregation mainly occurred where particular habitat features were present, such as piles of brushwood. Hence, it may be explained by the idiosyncrasy of the study site, particularly by a lack of favourable alternative microhabitats (mainly basking spots and hiding places in close proximity), rather than the presence of the wall lizard.

At the syntopic site, intraspecific interactions of wall lizards were more common than interspecific interactions with sand lizards. This may easily be explained by the different abundances of both species in the Tiefenbachtal (*P. muralis*: 73.1 ind./ha, *L. agilis*: 26.3 ind./ha each). Based on their higher density, wall lizards encounter and therefore interact more often with conspecifics, while the opposite might be true for *L. agilis*. A generally aggressive behaviour of wall lizards towards sand lizards was not confirmed, as the most common interaction was basking at a distance.

Conclusions

The introduction of wall lizards into a sand lizard population in the Tiefenbachtal and the limited availability of microhabitats at this site made us hypothesize that interspecific competition would lead to an observable niche shift of sand lizards. Based on behavioural observations on the wall lizard (Boag 1973, Edsman 1990), we also expected that aggressive interactions emanated mainly from the more territorial *P. muralis*. However, our observations do not confirm either of these assumptions. We are well aware of the limitations of our study design since it compares only two sand lizard populations, one with and one without syntopic introduced wall lizards. Furthermore our study was conducted in the summer months in which the territoriality of both species is less pronounced and resources (prey and basking spots) might be less limited than in spring. Nevertheless, we may at least conclude that no pronounced negative effect of the introduced species on the native species is detectable, at least not when considering the analysed niche dimensions and the time frame of this study (summer months).

Since there is evidence from other locations that introduced wall lizard populations may in fact affect native lizard populations (Allan et al. 2006, Bertram 2004, Mole 2008), more effort is needed to better understand the interactions between introduced wall lizards and the endangered sand lizard, which is strongly protected through the European Habitats Directive. Furthermore, it should be monitored whether the expansion of native wall lizards leads to a decline of sand lizards within typical *L. agilis* habitats in their native range (Baden-Württemberg, Rhineland-Palatinate, Saarland). Further studies on the potential predation of *P. muralis* on *L. agilis* juveniles by and their interspecific competition are needed, both *in situ* (e.g., during the mating season of both species, when territoriality is higher and therefore interspecific interactions might be more frequent) and experimentally.

Acknowledgements

We are grateful for the funding from the Hans-Schiemenz-Fonds of the Deutsche Gesellschaft für Herpetologie und Terrarienkunde e.V. for this project (to US, GD, AH, MV). Permits to conduct fieldwork were kindly issued by the Nature Conservation Authority of Nürtingen. We thank Norman Wagner for his help with the program POPAN and Ortwin Elle and Jessica Weyer for their help with the GIS analysis.

References

Allan, G. M., C. J. Prelypchan & P. T. Gregory (2006): Population profile of an introduced species, the common wall lizard (*Podarcis muralis*), on Vancouver Island, Canada. – Canadian Journal of Zoology, **84**: 51–57.

Avery, R. A. (1978): Activity patterns, thermoregulation and food consumption in two sympatric lizard species (*Podarcis muralis* and *P. sicula*) from Central Italy. – Journal of Animal Ecology, **47**: 143–158.

Bertram, N. (2004): Ecology of the Introduced European Wall Lizard, *Podarcis muralis*, near Victoria, British Columbia. – Thesis, Master of Science, BNRS, University College of the Cariboo.

Blanke, I. (2010): Die Zauneidechse. 2. überarb. Aufl. – Laurenti-Verlag, Bielefeld

Boag, D. A. (1973): Spatial relationships among members of a population of wall lizards. – Oecologia, **12**: 1–13.

Burnham, K. P. & D. R. Anderson (2002): Model Selection and Multi-model Inference: A Practical Information-Theoretic Approach. – New York (Springer).

Edsman, L. (1990): Territoriality and competition in wall lizards. – PhD thesis, Department of Zoology, University of Stockholm.

Fritz, K. (1987): Die Bedeutung anthropogener Standorte als Lebensraum für die Mauereidechse (*Podarcis muralis*) dargestellt am Beispiel des südlichen Oberrhein- und des westlichen Hochrheintals. – Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg, **41**: 427–462.

Font, E., P. Carazo, G. Pérez i de Lanuza & M. Kramer (2012): Predator-elicited foot shakes in wall lizards (*Podarcis muralis*): evidence for a pursuit-deterrent function. – Journal of Comparative Psychology, **126**: 87–96.

Gotelli, N. J. & G. L. Entsminger (2004): EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465. http://garyentsminger.com/ecosim/index.htm.

Laufer, H. (1998): Ein bedeutendes Vorkommen der Mauereidechse, *Podarcis muralis*, am Bahnkörper nördlich von Offenburg (Baden-Württemberg). – Zeitschrift für Feldherpetologie, **5**: 55–64.

Märtens, B. & W.-R. Grosse (1996): Fotografische Wiedererkennung bei Zauneidechsen (*Lacerta agilis* L., 1758) – Adulti und Juvenes. – Die Eidechse, **17**: 1–6.

Mole, S. (2008): An investigation into the effects of the western green lizard (*Lacerta bilineata*) and the common wall lizard (*Podarcis muralis*) introduced onto Boscombe Cliffs, Dorset, U. K. – Bachelor of Science thesis, Sparsholt College, unpubl.

Morisita, M. (1959): Measuring of the dispersion and analysis of distribution patterns. – Memoires of the Faculty of Science, Kyushu University, Series E. Biology, **2**: 215–235.

Münch, D. (2001): Gefährden allochthone Mauereidechsen autochthone Zaun- und Waldeidechsen-Populationen? – Dortmunder Beiträge zur Landeskunde (naturwiss. Mitt.), **35**: 187–190.

R Core Team (2012): R: A language and environment for Statistical Computing, Vienna, Austria, http://www.R-project.org, downloaded on 2011-12-07

Rose, B. (1982): Lizards Home Ranges: Methodology and Functions. – Journal of Herpetology, **16**: 253–269.

Schmidt-Loske, K. (1996): Fotographische Identifikation von *Podarcis muralis* Laur. 1768 – Möglichkeiten und Grenzen. – Die Eidechse, **7**: 7–12.

Schulte, U. (2008): Die Mauereidechse. – Laurenti-Verlag, Bielefeld.

Schulte, U. (2009): Expansion einer allochthonen Mauereidechsen-Population bei Leipzig. – Jahresschrift für Feldherpetologie und Ichthyofaunistik Sachsen, **11**: 2–10.

Schulte, U., B. Thiesmeier, W. Mayer & S. Schweiger (2008): Allochthone Vorkommen der Mauereidechse (*Podarcis muralis*) in Deutschland. – Zeitschrift für Feldherpetologie, **15**: 1–18.

Schulte, U., A. Hochkirch, S. Lötters, D. Rödder, S. Schweiger, T. Weimann & M. Veith (2012a): Cryptic niche conservatism among evolutionary lineages of an invasive lizard. – Global Ecology and Biogeography, **21**: 198–211.

Schulte, U., F. Gassert, P. Geniez, M. Veith & A. Hochkirch (2012b): Origin and genetic diversity of an introduced wall lizard population and its non-native cryptic congener. – Amphibia-Reptilia, **33**: 129–140.

Schulte, U., M. Veith & A. Hochkirch (2012c): Rapid genetic assimilation of native wall lizard populations (*Podarcis muralis*) through extensive hybridization with introduced lineages. – Molecular Ecology, **21**: 4313–4326.

Schwarz, C. J. & A. N. Arnason (2007): Jolly Seber models in MARK. – pp. 402–454 in: Cooch, E. & G. White (eds.): Program MARK – a gentle introduction, 8th Edition. – available at http://www.phidot.org/software/mark/docs/book/.

Steinicke, H. (2000): Ökologische Untersuchungen an einer isolierten Population der Mauereidechse, *Podarcis muralis* (Laurenti 1768) bei Leipzig. – Diplomarbeit Universität Halle-Wittenberg, unveröff.

Waitzmann, M. (1989): Untersuchungen zur Verbreitung, Ökologie und Systematik der Äskulapnatter – *Elaphe longissima* (Laurenti, 1768) im südlichen Odenwald und im Donautal unter besonderer Berücksichtigung aller anderen in den Untersuchungsgebieten auftretenden Reptilienarten. – Projektbericht, Zoologisches Institut Universität Heidelberg, unveröff.

Weber, H. (1957): Vergleichende Untersuchungen des Verhaltens von Smaragdeidechsen (*Lacerta viridis*), Maurereidechsen (*L. muralis*) und Perleidechsen (*L. lepida*). – Zeitschrift für Tierpsychologie, **14**: 448–472.

White, G. C. & K. P. Burnham (1999): Program MARK: survival estimation from populations of marked animals. – Bird Study, **46**: 120–139.

Winemiller, K. O. & E. R. Pianka (1990): Organization in natural assemblages of desert lizards and tropical fishes. – Ecological Monographs, **60**: 27–56.

Zimmermann, P. (1989): Zur Ökologie und Schutzproblematik der Mauereidechse (*Podarcis muralis*). – Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg, **64/65**: 221–236.