

Cave salamanders (*Speleomantes* spp.) in Germany: tentative species identification, estimation of population size and first insights into an introduced salamander

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Abstract. The pathways of introduction of non-native amphibians are diverse, as historically amphibians were used as pest control agents, food stock, or were introduced to perform research. Today, the pet trade is the main source for amphibian introductions into novel ranges. However, these introductions mainly concern anurans, whereas cases involving urodeles are less common. Since 2013, a population of European cave salamanders, *Speleomantes* spp. Dubois, 1984, is known to be present in Germany. However, knowledge on the size of this population is missing, and it is unknown to which of the similar-looking species of *Speleomantes* it belongs. Here, we applied loglinear capture-recapture models to estimate population size, and used a recently published photographic database, including more than 1000 images of all eight *Speleomantes* species, to determine the species identity of the German population. According to our estimates, the population consists of 170 to 485 individuals (\pm 134 to 320). Based on colour pattern the population most likely belongs to *S. italicus* (Dunn, 1923). We additionally provide the first evidence for reproduction and give further insights into this non-native salamander population.

Keywords. Plethodontidae, lungless salamanders, amphibians, non-native species, loglinear models

Introduction

The introduction of non-native amphibians outside their natural range often has strong negative impact on the local native fauna (Kraus, 2015; Measey et al., 2016). The pathways of introduction of non-native amphibians are diverse, as historically amphibians were used as pest control agents, food stock, or were introduced to perform research. Today, the pet trade is the main source for amphibian introductions into novel ranges (Kraus, 2009). Most cases of amphibian introduction into non-native areas relate to anurans, while cases involving urodeles are less common (Kraus, 2009; Fitzpatrick et al., 2010; Lunghi et al., 2018b).

The genus *Speleomantes* Dubois, 1984, commonly known as European cave salamanders, comprises eight

species, which are endemic to Italy and a small part of south-eastern France. Three species are distributed along the northern and central Apennine chain on the European mainland (*S. ambrosii* [Lanza, 1955], *S. italicus* [Dunn, 1923], *S. strinatii* [Aellen, 1958]), whereas the other five species (*S. flavus* [Stefani, 1969], *S. genei* [Temminck and Schlegel, 1838], *S. imperialis* [Stefani, 1969], *S. sarraabusensis* Lanza et al., 2001, and *S. supramontis* [Lanza et al., 1986]) endemic to Sardinia, Italy (Kwet, 2010; Glandt, 2015). Only two mainland species, *S. ambrosii* and *S. italicus*, come naturally into contact and give birth to hybrids in a small area (Ficetola et al., 2019). In past decades, *Speleomantes* were introduced to several non-native areas as well, which led to establishment of several reproducing populations (Lunghi et al., 2018b). *Speleomantes* are lungless, and require cold and moist environmental conditions for efficient cutaneous respiration (Lanza, 2006; Ficetola et al., 2018). The common name, cave salamanders, is misleading because they are not real troglobionts (obligate cave dwellers). *Speleomantes* often colonise subterranean habitats such as caves, but also other habitats like mines or crevices, where a cold and moist environment is provided throughout the year (Culver and Pipan, 2009). *Speleomantes* maintain stable populations and reproduce in those habitats (Lunghi et al., 2015; Lunghi et al., 2018a), mostly leaving them

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only to reach areas with high prey availability (Manenti et al., 2015; Lunghi et al., 2018c). Although, in several cases surface populations are known, such as those on the forest floor or on dry stone walls (Manenti, 2014; Costa and Salvidio, 2016).

Since 2013, the German herpetological community has been aware of an introduced *Speleomantes* population in the Weserbergland/Solling, Niedersachsen, Germany. However, identification of *Speleomantes* based on morphology alone is difficult (Kwet, 2010; Glandt, 2015) and thus the species identity of the German population is currently unknown, while studies on this non-native population are lacking. Further, it is unclear whether the species is established (i.e. a self-sustaining, reproductive population) at the non-native locality, or if it is just composed of a few individuals that persist there for some years. For this reason, we provide a tentative identification of the German *Speleomantes* population to species-level and estimate its population size. We used a recently published photographic database containing more than 1000 images of all eight European cave salamander species. For population size estimation, we used loglinear capture-recapture models for open populations.

Material and Methods

Study area. The study area is located in Holzminden, Lower Saxony, Germany (Fig. 1A). This area is located in between the natural area categories of 367.0 *Weseraue und Weserterrassen* and 370.0 *Nördlicher Solling* (Hövermann 1963). The biogeographical region is continental, but located close to the border of the Atlantic region in nearby North Rhine-Westphalia (Europäische Umwelt-Agentur, 2010). The present vegetation could be classified as *Asperulo-Fagetum*, following Pott (1992). It should be mentioned that our vegetation recording is not complete due to the late date of assessment, and presence of crucial species for determination, which were out of season like *Allium ursinum* L., could not be assessed. The salamander microhabitat (Figure 1B) is characterised by a scarp with some mosses and ferns (*Asplenium trichomanes* L.). Several blackberry (*Rubus fruticosus* L.) twigs hang over the scarp. The surrounding area is characterised by older trees (some up to hundreds of years). These trees are mainly Common beeches (*Fagus sylvatica* L.), some Common oaks (*Quercus robur* L.), few younger larches (*Larix decidua* Mill.) and some maple trees (*Acer*

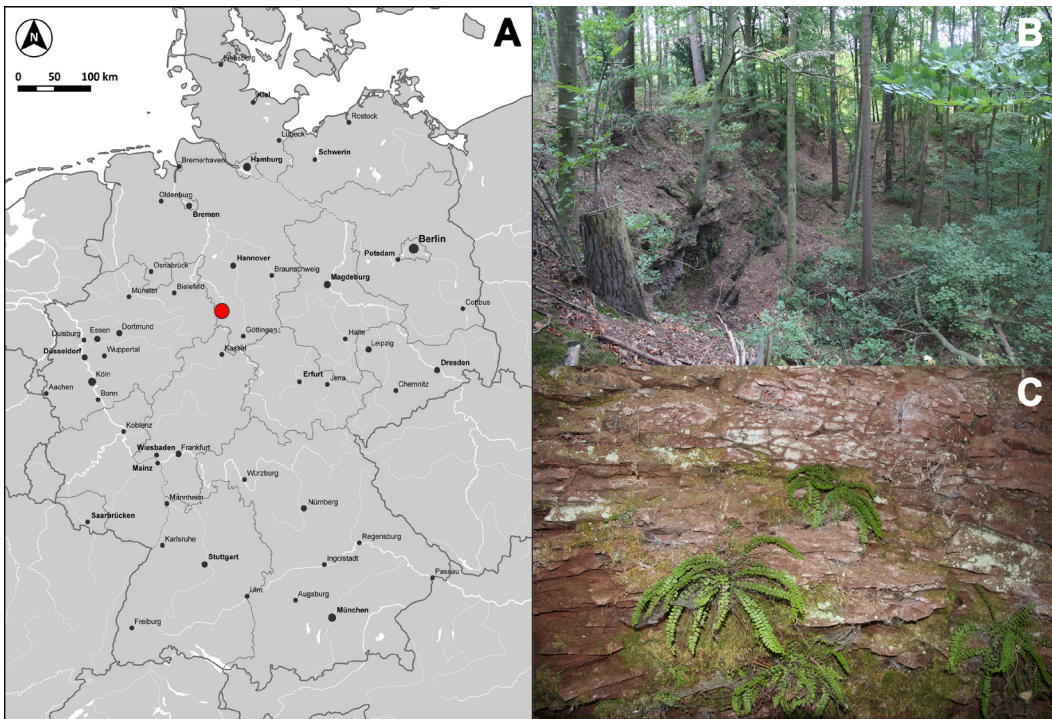


Figure 1. Study area: (A) location in Germany and (B and C) habitat.

pseudoplatanus L.). The herb layer mainly consists of blackberry and stinging nettle (*Urtica dioica* L.) with fewer woodruff (*Galium odoratum* [L.] Scop.) and honeysuckle (*Lonicera xylosteum* L.), which indicates a very eutrophic habitat. The ground is covered by a thick layer of mainly beech-foliage and some deadwood. The area is highly impacted by humans, which is indicated by a high amount of garbage, graffiti on parts of the scarp, self-made mountain bike trails, and a well-trodden path above and to the scarp. The closest buildings are just around 50 m away. The scarp has a maximum height of c. 6 meters and a length of c. 40 meters. Parts of the scarp are largely eroded and covered by leaf-litter. At some points, water is leaking out of the scarp, keeping it moist. Salamanders were only found in close vicinity to the scarp.

Study design. For species identification and estimation of population size, we selected a transect of 40 m length and 5 m width along the scarp. We visited the study area six times between 29 August 2020 and 31 October 2020 during cold (< 15 °C) nights with high probability of rain. Starting at sunset, we searched for salamanders until no more could be found along the transect. To avoid temporal autocorrelation and stress effects on the cave salamanders, surveys were separated by at least seven days. We searched for salamanders on the forest floor and in crevices along the scarp. Directly after collection, salamanders were photographed using a camera (Canon EOS 60D with EF-S 18-135 mm objective and a resolution of 5184x3456). We took several dorsal and dorsolateral pictures of each individual salamander, so that all individually specific markings in colour pattern were recorded. For this, each salamander was placed on a rock in their natural environment. We took the photos when the salamander was fully stretched moving forward. Further, the total length of each salamander was measured using a ruler, when the salamander was fully stretched. The ratio between adults and juveniles was determined according to Lunghi et al. (2020), which used the threshold of 68 mm of total length for European mainland cave salamanders when maturity is reached. To avoid direct recapture of the same individual, the salamanders were kept in a box prepared with moist leaf litter and moss from their natural habitat until the sampling was finished that day. After each transect run, all salamanders were released at their collection locality.

Species identification. Most *Speleomantes* species are similar in appearance and variable in colour pattern, which makes species identification based on small numbers of individuals difficult (Kwet, 2010;

Glandt, 2015). However, when looking at population level, tendencies in morphology and colour pattern characterise species (Lunghi et al., 2020). Accordingly, we used a recently-published photographic database (Lunghi et al., 2020) to compare photographic images of 70 different individuals from the German population with other *Speleomantes* populations throughout their native range. The database contains a total number of 1052 standardised images of dorsally photographed salamanders of all eight *Speleomantes* species (> 55 photographed specimens per species) from at least two different locations per species.

Estimation of population size. *Speleomantes* spp. show a complex dorsal pattern which is unique for each individual and stays stable when maturity is reached (Lunghi et al., 2019). This makes cave salamanders ideal subjects for capture-recapture studies. For individual identification, we chose up to 10 individually specific body markings (depending on the complexity of the individual colour pattern) to visually compare each salamander to salamanders of other sampling visits. When a salamander was assumed to be recaptured, all images of the specimen were compared in detail to ensure the identity. We used the *closure.test()*-function in the *secr*-package to test whether a population sampled by capture-recapture is closed to losses and gains over the period of sampling (Efford, 2020). Subsequently, we assumed an open population for further analyses. To estimate capture probabilities and the population size, we used the *openp()*-function of *Rcapture*-package (Baillargeon and Rivest, 2019) for R v. 3.6.2 (R Core Team, 2019). Following the guidelines of the *Rcapture*-package, we ran models setting unconstrained and equal capture probabilities (*openp()*-function set *m*-argument to “up” = unconstrained probabilities and “ep” = equal probabilities; Baillargeon and Rivest, 2019). The best model was selected according to the lowest Akaike Information Criterion (AIC). Furthermore, we performed a chi-square goodness of fit test based on the deviance. Considering the low number of recaptures, we performed a sensitivity analysis for the best model and simulated the effect of additional recaptures on the estimation of population size. For this task, we added a simulated capture occasion, where we ‘recaptured’ one to five additional salamanders (called sim 1 - 5).

Results

A total of 70 cave salamanders were caught at six sampling dates. The majority of salamanders could be caught only one time (n = 67), whereas three salamanders

were caught twice/recaptured once (Table 1). On each occasion, a mean of 12 ± 9 (range: 4 – 31) salamanders were caught. On average, the recaptured salamanders were caught 19 ± 8 (range: 14 – 28) days after their first capture. The measured salamanders’ total length ranged from 40 mm to 119 mm (mean: 92.6 ± 19.0 mm, $n = 58$). Fifty salamanders were above 68 mm and determined as mature individuals, while eight juveniles were found ($n = 58$).

Species identification. Sixty-nine out of 70 captured *Speleomantes* showed dark ventral colouration, with small lighter spots, and dark brown dorsal colouration interrupted by brown to red patterns of different brightness and density (Fig. 2A, B). Some specimens showed a grey stripe above the front legs. Within the red pattern, some individuals, especially smaller and probably juvenile to sub-adult salamanders, tended to show a colour gradient from spine to distal lateral body from red to yellow (Fig. 2C). A single individual showed distinctly paler colouration (Fig. 2D). According to Lanza (2006), all five Sardinian *Speleomantes* show light ventral colouration, whereas the three mainland species show a dark venter. Therefore, we assume that the German population derives from the European mainland. A comparison with the photo-database (Lunghi et al., 2020) supports this. Further, the only two species in the photo-database that appeared similar to almost identical in colour patterns and morphology to the German individuals were *S. ambrosii* and *S. italicus*. Two out of four *S. ambrosii* populations (see *S. ambrosii* populations 1 + 2 in Lunghi et al., [2020]) show a similar colour pattern, but the extent and intensity of their pattern is less while only few markings are dorsally centred or located between their hind limbs, which

characterise most German salamanders. Compared to the German population, an almost identical colour pattern and morphology was only found for three out of four *S. italicus* populations (see *S. italicus* populations 1 – 3 in Lunghi et al., [2020]). The fourth *S. italicus* population holds around a half of individuals with a similar pattern. For this reason, we conclude that the German *Speleomantes* population can most likely be assigned to *S. italicus*.

Estimation of population size. The closure test revealed that population closure over the period of sampling cannot be assumed ($z = -1.39$, $p = 0.08$). The two models, one set with unconstrained capture probabilities (“up”-model) and the other one set with equal capture probabilities (“ep”-model), showed significant goodness of fit ($p < 0.05$). According to the lowest AIC and an unrealistically high standard error in the “up”-model, we selected the “ep”-model to estimate the population size and the capture probabilities (Table 2). For all six sampling occasions, the averaged capture probabilities for the “ep”-model were 0.11 ± 0.07 . The estimated population size for the original dataset was 485 ± 320 individuals. However, the sensitivity analysis (sim1 - 5) revealed strong sensitivity of our dataset for additionally captured salamanders with a dropdown to 17–35 % of the originally estimated population size (Table 3).

Discussion

The German *Speleomantes* population is morphologically most similar to some populations of *S. italicus*. This species is native in the northern and central Apennines from the provinces Reggio Emilia to Lucca,

Table 1. Descriptive frequency statistics of capture-recapture trials on the German *Speleomantes* population: Number of salamanders captured i times ($i = 1, 2, 3, 4, 5, 6$), number of salamanders captured for the first and the last time on occasion i and number of salamanders captured on occasion i .

	Number of salamanders captured i times	Number of salamanders captured for the first time on occasion i	Number of salamanders captured for the last time on occasion i	Number of salamanders captured on occasion i
$i = 1$	67	10	9	10
$i = 2$	3	6	6	7
$i = 3$	0	4	4	4
$i = 4$	0	11	12	12
$i = 5$	0	9	8	9
$i = 6$	0	30	31	31



Figure 2. *Speleomantes* cf. *italicus* from the German population: (A) adult specimen with brown dorsal colouration, (B) adult specimen with red dorsal colouration, (C) juvenile and (D) adult specimen with pale colouration. Photographs by Carl-Henning Loske.

southwards to Pescara at 80 to 1600 m elevation (Frost, 2020). The German population is c. 800 km away from the species' known native range. Therefore, the German population can be seen as non-native and also as the northernmost European cave salamander population. Further, Lucente et al. (2016) mention that in past decades some translocation/introduction experiments, often scientifically unpublished, were made throughout the mainland part of European cave salamanders' range. Lunghi et al. (2018b) also mention that six of these introduction experiments are known, which all seem to

be established populations, partially composed by two or also three *Speleomantes* species from the European mainland. The latter authors also note the existence of the German *Speleomantes* population as an example of a translocation experiment, but without any other details.

Speleomantes species from the European mainland are extremely variable in their pattern and colouration and the photographic database does not include all known populations (i.e. populations of *S. ambrosii bianchii*). Furthermore, there might be a chance that the German population is composed of hybrids by two or even more

Table 2. Model output for the *open population* models: Deviance, degrees of freedom (df), AIC, p-value of chi-square goodness of fit test and estimated abundance \pm standard error (SE) for the two models, one set with unconstrained probabilities, the other one set with equal probabilities.

	Deviance	df	AIC	p-value	Estimated abundance \pm SE
Unconstrained probabilities	1.70	50	57.93	<0.001	236 \pm 675521
Equal probabilities	4.07	53	54.30	<0.001	485 \pm 320

Speleomantes species. Particularly, hybrids of *S. italicus* and the very similar looking *S. ambrosii* might be nearly impossible to detect using morphological characteristics alone. Thus, future studies that include genetic analysis will help to clarify this issue definitely.

Of the 70 individuals caught, one showed a distinctly paler colouration than the other conspecifics (Fig. 2D). Cases of anomalies in colouration are known from several amphibians including also the cave salamanders *S. sarrausensis*, *S. flavus* and *S. supramontis*, from which cases of albinism, leucism and melanism have been reported (Lunghi et al., 2017a, b).

Considering the modest number ($n=70$) of salamanders caught, with only three recaptures, population size estimates showed strong variation (485 ± 320) and sensitivity analysis revealed that the estimation is highly sensitive to additional recaptures (Table 3). Also, the capture probabilities of 0.11 ± 0.07 seem high, considering that only three out of 70 salamanders were recaptured. The model revealed that our dataset was insufficient to clearly estimate the population size of the German population. However, sensitivity analysis also showed that the dropdown in the estimated population size strongly decreases when two or more additional recaptures would be made (sim2: 24 %, sim3: 20 %, sim 4: 18 %, sim 5: 17 %; Table 3). Nevertheless, it seems unrealistic that two to five additional recaptures might be achieved during a single sampling occasion, especially without any new captures. Therefore, we assume that the realistic population size might be set between 170 and 485 (sim1 and sim0) individuals.

The German population was first recognized in 2013. However, it can be assumed that the population occurred there for many more years, or even decades. During our field work, we could find a pregnant female and several juvenile specimens of c. 40 mm total length, which is the

first evidence for reproduction in this area. Therefore, the German *Speleomantes* can be characterised as an established, reproducing population. The broad variation in colour pattern could be an indication for a broad base of founder animals. Unfortunately, we could not clarify the pathway of introduction. We assume that a private amphibian enthusiast released some founder animals. Non-native amphibians can have strong impacts on the native fauna including other amphibians (Ryan et al., 2009; Measey et al., 2015, 2016; Courant et al., 2018). At the time of the investigation the species was non-invasive according to the definitions of Ricciardi and Cohen (2006) because the German population has been confined to a small area since it was first detected. However, several authors have shown that long time-periods can pass before non-native vertebrates first appear in the wild or even become invasive (e.g., Nehring et al., 2015; Toledo and Measey, 2018). For amphibians, it is known that this phenomenon also known as invasion debt, the time span between the introduction and establishment phase of an invasion, can be highly variable (35 years for *Xenopus laevis* [Daudin, 1802], while five years for *Sclerophrys gutturalis* [Power, 1927], introduction debt + establishment debt + spread debt; for details see Van Sittert and Measey, 2016; Vimercati et al., 2017). Therefore, this requires monitoring of non-native species in order to be able to evaluate the potential impact of each taxon over time. So far, there is no official open access platform to report ‘new’ alien species but approaches to assess the invasiveness of wild non-native species in Germany (Nehring et al., 2015; Rabitsch and Nehring, 2017). Interestingly, we found several native amphibian species (*Bufo bufo* [Linnaeus, 1758], *Ichthyosaura alpestris* [Laurenti, 1768], *Lissotriton helveticus* [Razoumowsky, 1789], *Lissotriton vulgaris* [Linnaeus, 1758], *Salamandra salamandra* [Linnaeus, 1758]), some in high numbers, syntopic with *Speleomantes*. Particularly, several *I. alpestris* and *S. salamandra* were found in the same crevices as the cave salamanders. Furthermore, the cave salamanders seem to be restricted to the collection transect and its close vicinity. After intense survey at two other scarps (distance of 150–200 m), which we assumed to be also suitable habitats, no *Speleomantes* could be found. For cave salamanders, it has been shown that their dispersal ability is very limited and they seem to show a high site fidelity even if other suitable habitat is available in close proximity (Salvidio, 2013; Lunghi and Bruni, 2018). However, we conclude that further investigation on the potential impact on native fauna and the potential dispersal ability is needed.

Table 3. Estimated population size (mean \pm SE) of the original dataset (sim0) and the sensitivity analysis (sim1 - 5) for the “ep”-model.

	Population size	Percentage [%]
Sim 0	485 \pm 320	100
Sim 1	170 \pm 134	35
Sim 2	112 \pm 52	24
Sim 3	96 \pm 30	20
Sim 4	88 \pm 21	18
Sim 5	84 \pm 16	17

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References

- Baillargeon, S., Rivest, L.P. (2007): Recapture: Loglinear models for capture-recapture in R. *Journal of Statistical Software* **19**(5): 1–31.
- Costa, A., Crovetto, F., Salvidio, S. (2016): European plethodontid salamanders on the forest floor: Local abundance is related to fine-scale environmental factors. *Herpetological Conservation & Biology* **11**: 344–349.
- Courant, J., Secondi, J., Vollette, J., Herrel, A., Thirion, J.M. (2018): Assessing the impacts of the invasive frog, *Xenopus laevis*, on amphibians in western France. *Amphibia-Reptilia* **39**(2): 219–227.
- Culver, D.C., Pipan, T. (2009): The biology of caves and other subterranean habitats. Oxford, Oxford University Press.
- Efford, M.G. (2020): secr: Spatially explicit capture-recapture models. R package version 4.3.3. <https://CRAN.R-project.org/package=secur>
- Europäische Umwelt-Agentur (2010): Natura 2000 in der kontinentalen Region. Available at https://ec.europa.eu/environment/nature/info/pubs/docs/biogeos/Continental/KH7809635DEC_002.pdf (Accessed 5 Jan 2021)
- Ficetola, G.F., Lunghi, E., Canedoli, E., Padoa-Schioppa, E., Pennati, R., Manenti, R. (2018): Differences between microhabitat and broad-scale patterns of niche evolution in terrestrial salamanders. *Scientific Reports* **8**: 10575.
- Ficetola, G.F., Lunghi, E., Cimmaruta, R., Manenti, R. (2019): Transgressive niche across a salamander hybrid zone revealed by microhabitat analyses. *Journal of Biogeography* **46**(7): 1342–1354.
- Fitzpatrick, B.M., Johnson, J.R., Kump, D.K., Smith, J.J., Voss, S.R., Shaffer, H.B. (2010): Rapid spread of invasive genes into a threatened native species. *Proceedings of the National Academy of Sciences of the United States of America* **107**(8): 3606–3610.
- Frost, D.R. (2020): Amphibian species of the world: An online reference. Version 6.1. Available at <http://research.amnh.org/herpetology/amphibia/index.html>. American Museum of Natural History, New York, USA. Accessed on November 2020.
- Glandt, D. (2015): Die Amphibien und Reptilien Europas: Alle Arten im Porträt. Leipzig, Germany, Quelle & Meyer.
- Höfermann, J. (1963): Die naturräumlichen Einheiten auf Blatt 99. Göttingen, Germany, Institut für Landeskunde.
- Kraus, F. (2009): Alien reptiles and amphibians: A scientific compendium and analysis. Dordrecht, Springer.
- Kraus, F. (2015): Impacts from invasive reptiles and amphibians. *Annual Review of Ecology, Evolution, and Systematics* **46**: 75–97.
- Kwet, A. (2010): Reptilien und Amphibien Europas: 190 Arten mit Verbreitungskarten. Stuttgart, Germany, Kosmos.
- Lanza, B. (2006): A review of systematics, taxonomy, genetics, biogeography and natural history of the genus *Speleomantes* Dubois, 1984 (Amphibia, Caudata, Plethodontidae). *Atti del Museo Civico di Storia Naturale di Trieste* **52**: 5–135.
- Lucente, D., Renet, J., Gailledrat, M., Tillet, J., Nascetti, G., Cimmaruta, R. (2016): A new population of European cave salamanders (genus *Hydromantes*) from west-central France: Relict or introduction? *Herpetological Bulletin* **138**: 21–23.
- Lunghi, E., Bruni, G. (2018): Long-term reliability of Visual Implant Elastomers in the Italian cave salamander (*Hydromantes italicus*). *Salamandra* **54**(4): 283–286.
- Lunghi, E., Corti, C., Manenti, R., Barzaghi, B., Buschetti, S., Canedoli, C., et al. (2018a): Comparative reproductive biology of European cave salamanders (genus *Hydromantes*): Nesting selection and multiple annual breeding. *Salamandra* **54**(2): 101–108.
- Lunghi, E., Ficetola, G.F., Barzaghi, B., Vitillo, C., Mulargia, M., Manenti, R. (2017a): Melanism in European plethodontid salamanders. *Spixiana* **40**: 157–160.
- Lunghi, E., Giachello, S., Zhao, Y.H., Corti, C., Ficetola, G.F., Manenti, R. (2020): Photographic database of the European cave salamanders, genus *Hydromantes*. *Scientific Data* **7**(1): 171.
- Lunghi, E., Guillaume, O., Blaimont, P., Manenti, R. (2018b): The first ecological study on the oldest allochthonous population of European cave salamanders (*Hydromantes* sp.). *Amphibia-Reptilia* **39**(1): 113–119.
- Lunghi, E., Manenti, R., Ficetola, G.F. (2015): Seasonal variation in microhabitat of salamanders: environmental variation or shift of habitat selection? *PeerJ* **3**: e1122.
- Lunghi, E., Manenti, R., Mulargia, M., Veith, M., Corti, C., Ficetola, G.F. (2018c): Environmental suitability models predict population density, performance and body condition for microendemic salamanders. *Scientific Reports* **8**: 7527.
- Lunghi, E., Monti, A., Binda, A., Piazzi, I., Salvadori, M., Cogoni, R., et al. (2017b): Cases of albinism and leucism in amphibians in Italy: New reports. *Natural History Sciences* **4**(1): 73–80.
- Lunghi, E., Romeo, D., Mulargia, M., Cogoni, R., Manenti, R., Corti, C., et al. (2019): On the stability of the dorsal pattern of European cave salamanders (genus *Hydromantes*). *Herpetozoa* **32**: 249–253.
- Manenti, R. (2014): Dry stone walls favour biodiversity: A case-study from the Appennines. *Biodiversity and Conservation* **23**(8): 1879–1893.
- Manenti, R., Lunghi, E., Ficetola, G.F. (2015): The distribution of cave twilight-zone spiders depends on microclimatic features and trophic supply. *Invertebrate Biology* **134**(3): 242–251.
- Measey, J., Vimercati, G., De Villiers, F.A., Mokhatla, M.M., Davies, S.J., Edwards, S., et al. (2015): Frog eat frog: Exploring variables influencing anurophagy. *PeerJ* **3**: e1204.
- Measey, J., Vimercati, G., De Villiers, F.A., Mokhatla, M., Davies, S.J., Thorp, C.J., et al. (2016): A global assessment of alien

- amphibian impacts in a formal framework. *Diversity and Distributions* **22**(9): 970–981.
- Nehring, S., Rabitsch, W., Kowarik, I., Essl, F. (2015): Naturschutzfachliche Invasivitätsbewertung für in Deutschland wildlebende gebietsfremde Wirbeltiere. *BfN-Skripten* **409**: 1–222.
- Pott, R. (1992): *Die Pflanzengesellschaften Deutschlands*. Stuttgart, Germany, Ulmer.
- Rabitsch, W., Nehring, S. (2017): Naturschutzfachliche Invasivitätsbewertung für in Deutschland wild lebende gebietsfremde aquatische Pilze, Niedere Pflanzen und Wirbellose Tiere. *BfN-Skripten* **458**: 1–220.
- R Core Team (2019): *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at <https://www.R-project.org/>.
- Ricciardi, A., Cohen, J. (2006): The invasiveness of an introduced species does not predict its impact. *Biological Invasions* **9**(3): 309–315.
- Ryan, M.E., Johnson, J.R., Fitzpatrick, B.M. (2009): Invasive hybrid tiger salamander genotypes impact native amphibians. *Proceedings of the National Academy of Sciences of the United States of America* **106**(27): 11166–11171.
- Salvidio, S. (2013): Homing behaviour in *Speleomantes strinatii* (Amphibia Plethodontidae): A preliminary displacement experiment. *Northwestern Journal of Zoology* **9**: 429–432.
- Schulz, V., Gerhardt, P., Stützer, D., Seidel, U., Vences, M. (2021): Lungless salamanders of the genus *Speleomantes* in the Solling, Germany: Genetic identification, Bd/Bsal-screening, and introduction hypothesis. *Herpetology Notes* **14**: 421–429.
- Toledo, L.F., Measey, J. (2018): Invasive frogs in São Paulo display a substantial invasion lag. *BioInvasions Records* **7**(3): 325–328.
- Van Sittert, L., Measey, J. (2016): Historical perspectives on global exports and research of African clawed frogs (*Xenopus laevis*). *Transactions of the Royal Society of South Africa*, **71**(2), 157–166.
- Vimercati, G., Hui, C., Davies, S.J., Measey, J. (2017): Integrating age structured and landscape resistance models to disentangle invasion dynamics of a pond-breeding anuran. *Ecological Modelling* **356**: 104–116.