



universität
wien

MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

„A recapture study on two fire salamander populations in
contrasting habitats in the Vienna woods“

verfasst von / submitted by

Stephan Burgstaller, BSc

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of
Master of Science (MSc)

Wien, 2019 / Vienna 2019

Studienkennzahl lt. Studienblatt /
degree programme code as it appears on
the student record sheet:

A 066 831

Studienrichtung lt. Studienblatt /
degree programme as it appears on
the student record sheet:

Masterstudium Zoologie

Betreut von / Supervisor:

Doz. Dr. Günter Gollmann

Acknowledgements

My gratitude goes out to my supervisor Günter Gollmann for aiding me with the work on this thesis, even though it took me an unusual amount of time to finish. I thank Walter Hödl for the help in organizing my office at the university, helping me getting the thesis topic accepted and his everlasting motivation. Vital for this research was the work of Christoph Leeb, who kindly offered me a large portion of data, which was used in this study. Max and Eva Ringler were a big help during several phases of data analysis, which had a positive influence on the study's quality. The students who participated in the field course "Populationsbiologie heimischer Amphibien", during the sampling periods, were an essential help with data collection. Finally, I want to thank the University of Vienna and the Department of Integrative Zoology for providing me the opportunity to work on a topic that is not only of scientific but, to me also of personal interest, that challenged me and let me grow as a researcher.

Table of contents

Abstract	6
Introduction	7
Methods	9
Species.....	9
Study sites	9
Data collection.....	11
Data preparation	11
Demographic analysis	13
Spatial activity	15
Results	16
Capture data.....	16
Demographic estimations	20
Spatial activity	23
Discussion	26
Goodness-of-fit testing	26
Survival and emigration rates	26
Recapture rates and probabilities.....	27
Breeding frequency	27
Population density	27
Spatial activity	28
Conclusion	29
References	30
Attachments	35
Zusammenfassung	39

Abstract

Understanding amphibians' population dynamics is vital to aid their conservation. New data on the migratory activity and site fidelity of *Salamandra salamandra*, but especially their adaptations to different habitats, led to much discussion. This capture-recapture study compared the population structure of two populations of *S. salamandra* in the Vienna woods, occurring in habitats that vary in terms of humidity, type of breeding waters, amount of barriers and topographical structure. Salamanders were captured, photographed and immediately released. From the capture-recapture data demographic parameters were estimated, using the program MARK. The capture locations were recorded, using ArcGIS. The distances were used to calculate movement distances and home ranges. Females and males were tested for differences in demographic parameters and spatial activity. The population density at the site located in a beech forest traversed by a stream was more than twice as high as at the site located in an oak-hornbeam forest with stagnant water bodies. Annual apparent survival was mostly high (~ 0.85). Only the estimate for females from the low density site was rather low (~ 0.60), indicating a high rate of emigration or mortality. Movement distances and home ranges showed no significant differences between sexes and were rather similar across sample sites. Movement distances over a two-year interval were not significantly longer than over one-year intervals, giving no sign of a shift of home ranges in a continuous direction.

Key words: capture-recapture, habitat effect, home range, population density, *Salamandra salamandra*, site fidelity, Vienna woods

Introduction

Amphibian populations throughout Europe are under increasing pressure by habitat loss and fragmentation (Cushman 2006, Harper et al. 2008, Arntzen et al. 2017) and, especially in case of *S. salamandra*, lethal fungal epidemics (Martel et al. 2013, Spitzen-van der Sluijs et al. 2016, Bower et al. 2017). Therefore, it is important to understand their population dynamics in diverse habitats. Breeding waters are of special interest (Manenti et al. 2009), as they can constrain population density (Beebee et al. 1996) and limit the extent of the species habitable area. They may also influence the rates of emigration from the habitat.

Important variables for describing a population's condition are, among others, density, survival, recruitment, emigration and immigration (Duellman & Trueb 1994). To assess these aspects of a population's condition capture-recapture studies have become a widely used method. In the last few decades, a multitude of model structures has been created (Lebreton et al. 1992, Pollock 2000, Chao 2001, Lukacs & Burnham 2005, Sandercock 2006) to estimate the demographic parameters of interest. Models with the same structure can be tested against each other, to determine how well the data support them, and thus, their respective assumptions (Schmidt et al. 2002). This includes, for example, assumptions about the existence of seasonal differences or differences according to sex, age etc.

Traditionally, terrestrial salamanders have been described as having a rather strong site fidelity (Feldmann 1967, Marvin 2001, Bonato & Fracasso 2003, Rebelo & Leclair 2003). Only occasional reports of individuals migrating large distances existed until 2007 (Klewen 1985). Several more recent studies suggested that populations of *S. salamandra* (Schmidt et al. 2007, Schulte et al. 2007) and *S. infraimmaculata* (Bar-David et al. 2007) had a larger proportion of individuals with higher mobility and larger home ranges than previously thought. Schmidt et al. (2007) even concluded that *S. salamandra* was highly mobile or at least had a large proportion of non-stationary individuals, so-called floaters. These seemingly contradictory results already indicated a high variability in movement activity and site fidelity between populations. This was later also proposed by Schmidt et al. (2014). In a recent study Hendrix et al. (2017) examined movement behavior of two subpopulations from Kottenforst in West Germany. The pond-adapted subpopulation showed a higher variability in moving distances and home range sizes and more long distance movements than the stream-adapted subpopulation. They concluded that adaptations regarding movement activity, be they genetic or plastic, can even occur within the same population.

Abundance of terrestrial salamanders can be greatly affected by water availability (Grover 1998). Water easily permeates amphibian skin (Shoemaker & Nagy 1977). This makes terrestrial living species prone to dehydration. The environment's humidity influences how fast water evaporates from the animals' skin and how well they can rehydrate through the soil (Spight 1967).

In the present study two populations of *S. salamandra* inhabiting contrasting habitats and therefore facing different ecological pressures and constraints were compared. One habitat, Neuwaldegg, is a beech forest, which is traversed by a stream and has little to no barriers to potential neighboring habitats. The other one, Maurer Wald, is an oak-hornbeam forest. It is located between several structures that might serve as barriers. Maurer Wald is restricted by a wall in the north-west, by a road in the south-west and by urban area in the east. The only existing water bodies are stagnant. Oak-Hornbeam forests usually are located in areas too dry for beech trees to grow, indicating lower precipitation or higher evaporation rates (Ellenberg 1988).

Earlier studies conducted on these two populations addressed differences in the larvae's morphometrics (Keckeis 2013) and in size and body condition of both larvae and adults (Mayerhofer 2013). Mayerhofer (2013) found that adult individuals from Maurer Wald on average had a lower body condition. Keckeis (2013) showed that in the same habitat larvae were larger than the ones from the stream population in Neuwaldegg, which can reflect higher food availability but might also be a sign of high intraspecific competition (Csilléry & Lengyel 2004). From 2011 to 2013 a camera trap study was carried out in Maurer Wald investigating the salamanders' hibernation activity (Leeb 2013, Leeb et al. 2013). A mass hibernation site was found, for which the adult salamanders showed high site fidelity. Approximately 85 % of recorded adult salamanders returned to the hibernation site in the following year. The catchment area for this hibernation site was estimated to have a radius of over 250 m.

Considering previous studies and the habitats' ecological conditions, it was expected that the population density in Maurer Wald would be lower. Due to the isolation by physical barriers, the emigration rate might be lower as well in Maurer Wald. Because the study took place in the breeding season, females were expected to show larger movement distances and home ranges than males in both habitats.

To test these assumptions capture-recapture data from both study sites were analyzed. Demographic parameters were estimated (e.g. population density, apparent survival, recapture probability) using the program MARK (White & Burnham 1999, <http://www.phidot.org/software/mark/index.html>). From the capture locations movement distances and minimum home ranges were calculated.

Methods

Species

The fire salamander (*Salamandra salamandra*) (Figure 1) is Europe's largest salamander species, reaching a total length of up to 20 cm and an age of up to 20 years in central Europe (Thiesmeier 2004). It inhabits broadleaf or mixed forests (beech, oak and hornbeam trees predominant) with running waters, which are utilized for larvae deposition. Sometimes also stagnant water bodies are utilized. After metamorphosis, the animals are terrestrial and as adults (after 3-5 years) usually only visit the water again to deposit their offspring (Thiesmeier 2004). In Europe the taxon consists of various (exact number is still topic of discussion) subspecies, of which only the nominate form, *S. s. salamandra*, occurs in Austria (Cabela et al. 2001). Each individual carries a unique dorsal pattern of yellow to orange spots and lines, which appear with metamorphosis and only change slightly during their ontogeny (Balogová et al. 2016). This makes it possible to identify the animals individually (Figure 3).



Figure 1: An adult fire salamander found in Neuwaldegg, one of the two sampling sites.

Study sites

The study was carried out at two sites in the Vienna Woods in the west and northwest of Vienna (Figure 2).

The first of the two is referred to as Neuwaldegg, although a major part of it is located across the north-western border of Vienna to Lower Austria and thus belongs to the south-eastern part of Kierlinger Forst (WGS84, 48.249°N, 16.263°E). It is part of the protected area Biosphärenpark Wienerwald and borders to the urban area of Vienna in the southeast. The forest area continues to the north and west for at least two kilometres without any major barriers that might hinder free movement. The study site itself extends over an area of 7.53 ha and is located along both sides of a creek, which runs through a steep ravine (Figure 2A). This creek, which the salamanders use for larvae deposition, is the only water body in the study area, although there are several creeks and temporary lentic water bodies in the surrounding area that are also used for larvae deposition.

The second study site, Maurer Wald, is located in the south-west part of Vienna (WGS84, 48.152°N, 16.247°N). It lies between Lainzer Tiergarten, which is restricted by a wall, in the north-west, a road (Gütenbachstraße) in the south-west and the urban area of Vienna in the east. Maurer Wald is also part of Biosphärenpark Wienerwald and belongs



Figure 2: Maps of the two study sites. Map A shows the study site in Neuwaldegg and Map B the study site in Maurer Wald. Bold lines mark the borders of the sampling areas. Map C shows where the two study sites are located in the Vienna Woods; 'A' marks Neuwaldegg; 'B' marks Maurer Wald. The area within the borders of Vienna is marked with a red overlay. Maps were used from the site <https://www.openstreetmap.org>.

to an area protected under the European Natura 2000 conservation program (<http://ec.europa.eu/environment/nature/natura2000>). There it is indexed under the name Landschaftsschutzgebiet Liesing (site code: AT1303000). This site differs from the study site in Neuwaldegg in several aspects. First, it is lacking any running water. The only existing water bodies are temporary pools, which usually are filled with water in early spring. Some dry out again during summer. The closest suitable running water is the stream Gütenbach at a distance of approximately one kilometre. Further, compared to Neuwaldegg, the site's surface is rather flat. There are little to no slopes with crevices, which often serve the salamanders as hibernation locations. Considering the before mentioned barriers, Maurer Wald is more isolated than Neuwaldegg and migration to other areas is expected to be more difficult. Although the actual sampled area in Maurer Wald was larger, only an area (Figure 2B) with a size of 4.96 ha was sampled on a regular basis and therefore was used in this study.

The forest in Neuwaldegg consists mainly of beech trees, whereas in Maurer Wald oak-hornbeam forest is predominant. The latter usually grows at locations with either less precipitation, or a higher mean temperature during summer months, resulting in a higher evaporation rate (Ellenberg 1988).

Data collection

At Neuwaldegg data sampling took place on 20 occasions (29.03. – 07.06.) in 2010, on 13 occasions (17.03. – 09.06.) in 2011 and on 16 occasions (27.03. – 09.06.) in 2012, at varying times of the day. The salamanders were collected along the trails leading along each side of the creek's ravine. All salamanders that were spotted from the trails were captured.

At Maurer Wald sampling data were available for both spring and autumn season up until 2015. For better comparability only data from approximately the same sampling periods as in Neuwaldegg were used. They took place on 8 occasions (31.03. – 16.05.) in 2010, on 13 occasions (02.03. – 23.06.) in 2011 and on 14 occasions (13.03. – 23.06.) in 2012 at varying times of the day. In contrast to the sampling site in Neuwaldegg the whole research area was evenly searched.

The date, time, sex and location of each captured animal were noted. For future identification, a picture of the animals' dorsal pattern was taken, using a compact camera (Olympus Tough TG-810). Sexing was done by examining the animals' cloaca (Nöllert & Nöllert 1992) and general habitus (i.e. swollen belly). To reflect the certainty of determining the animal's sex, a rating scale was introduced, which ranged from '0' to '3', with '0' meaning 'undeterminable' and '3' meaning 'very high certainty'. If the sexing of recaptures contradicted earlier data, the sex with the higher certainty rating was chosen. The coordinates of the capture location were determined and digitally saved, using the geoinformation program ArcMap, running on a portable device (Ashtech MobileMapper 10). All the mentioned data (including the photo ID) were entered into the MobileMapper and saved as a set of data, corresponding to the points of the individuals' capture locations.

Data preparation

Picture preparation and individual identification

A photo database was established and each individual salamander was given a unique ID. The photos taken of the animals at each capture event were compared to the photos of each individual in the database (Figure 3). The photos' contrast and brightness were adjusted using GNU Image Manipulation Program 2.8 (www.gimp.org). The comparison of the dorsal patterns and consecutive individual identification was carried out using the pattern-recognition software WILD-ID (Bolger et al. 2012). If WILD-ID did not yield a matching photo from the database, the photo was compared manually to ensure the correct identification of the animal. If a matching photo was already present in the

database, the capture was marked as a recapture, otherwise the animal was included in the photo database and marked with a new individual ID.



Figure 3: An individual captured in 2010 (above) and recaptured in 2012 (below) in Neuwaldegg. Exact dates of the capture events are provided.

Capture histories

As a starting point for further analysis, the capture-recapture (CR) data were manually compiled into a capture history for each study site. The simplest form of a capture history is a two-dimensional matrix, with one row per individual and one column per capture occasion. To signal an individual's capture on a certain occasion, the corresponding position is filled with the number '1'. If it was not captured, the position is filled with the number '0'. This is the basic data layout most CR-data-processing programs work with, including MARK (White & Burnham 1999, <http://www.phidot.org/software/mark/index.html>), which was used in this study.

Geographic data

To visualize the capture locations of each individual and process the geographic data in general, ArcMap 10.6 was used. Point, line and polygon layers were used to display capture locations, movement distances and areas (i.e. research areas), respectively. The geographic coordinate system WGS84 was used. To make distance and area calculations possible, the concerning layers were projected to the WGS84 UTM 33N system. To visualize home ranges for each individual captured three or more times Minimum Convex

Polygons (MCP; Powell 2000) were constructed, using the Home Range Tools 2.0 Extension for ArcGIS (Rodgers et al. 2015, <http://flash.lakeheadu.ca/~arodgers/hre/>).

Demographic analysis

Estimated parameters

In this study four real (not derived) parameters were estimated to describe the populations' structure. Apparent survival probability (φ_i), recapture probability (p_i), super population size (N) and probability of entry (p_{ent}).

The apparent survival probability (φ_i) is the probability that individuals found at time i are still present and alive at time $i+1$. This parameter combines the true rate of survival (s) with the rate of permanent emigration (e) in the following manner

$$\varphi_i = s * (1 - e)$$

The recapture probability (p_i) is the probability to capture an individual, found on a previous occasion, at time i , alive. The super population size (N) is the estimated total number of individuals, which were present at some point during the total timespan of the analysis. Probability of entry (p_{ent}) is the proportion of the super population that entered the population on occasion i , through either reproduction or immigration. This parameter is mainly used to calculate the net population sizes (N_i). Net population sizes (N_i) are derived parameters and are the number of individuals present at the sampling site on occasion i .

Model building: Basics

To estimate φ_i and p_i Cormack-Jolly-Seber (CJS) models were used (Lebreton et al. 1992). To estimate N and p_{ent} the POPAN model structure (Schwarz & Arnason 1996) was applied. It contains all four types of real parameters described.

These parameters can be modelled as either constant or dependent on various attributes. Most common are time- and group-dependencies. In this study, a distinction was made between females and males, therefore mentioning of groups, in context of demographic analysis, always refers to the two sexes.

All sets of models (CJS and POPAN for each sample site) were fitted using MARK. Intervals between capture occasions were entered as number of days divided by 30 to calculate estimates for monthly apparent survival (30-day-intervals are treated as one month). Before fitting more specific models, the fully time- and group-dependent models – the most general ones – were tested for goodness-of-fit.

Goodness-of-fit testing

Heterogeneity in detection rates (Gimenez et al. 2017) can exist, which might be caused by animals living near the edge of the sampling area and periodically leaving and re-entering it at various capture occasions (Schmidt et al. 2007). It was suspected that

especially at the sampling site in Neuwaldegg, with its relatively narrow sampling area, this effect might have a considerable effect on data consistency. To test for detection rate heterogeneity in the data, program RELEASE was used on the data of both sampling sites. RELEASE is included in MARK and utilizes the same type of capture history. It examines the fit of the fully time- and group-dependent model (ϕ_{t^*g}, p_{t^*g}) of the respective data set. The results indicated good fit for both data sets, both in total and underlying groups (Table 1).

Table 1: Goodness-of-fit test results calculated with program RELEASE for the fully time- and group-dependent models for each site's total data set and their underlying groups (Female/Male).

Sample site	Group	χ^2	df	p
Neuwaldegg	Female	28.5784	56	0.9991
	Male	37.6530	54	0.9556
	Total	66.2314	110	0.9997
Maurer Wald	Female	2.5717	15	0.9998
	Male	8.9251	35	1.0000
	Total	11.4968	50	1.0000

Model building: Continued

As the goodness-of-fit test delivered no signs of detection rate heterogeneity, more specific models, which are nested in the fully time- and group-dependent model (ϕ_{t^*g}, p_{t^*g}), could be fitted. The super population size parameter (N) in POPAN models was modelled as constant or varying between groups. Probability of entry (p_{ent}) always was modelled as varying through time. The other parameters were either modelled as constant, varying through time, varying between groups or both, time- and group-variant. This led to 16 different possible CJS models for each site. For Neuwaldegg five and for Maurer Wald two of those models could not be computed by MARK (most of them had a relatively high number of parameters). Of the 32 possible POPAN models, 16 models (all those with time-dependent apparent survival) could not be computed or yielded the warning "Numerical convergence suspect" for the data set from Neuwaldegg. For the data set from Maurer Wald, this happened only with four POPAN models. Those models were excluded from further analysis. By using the Akaike's Information Criterion corrected for small sample sizes (AIC_c), each model's relative support was determined (Burnham et al. 1995, Anderson & Burnham 1999, Akaike 2011).

To estimate the annual recapture probability (p_a), two additional sets of CJS models were built. Capture occasions within years were pooled and treated as a single capture occasion separated by equal time intervals. Eight models were fit for each sample site. ϕ_i was modelled as constant or group dependent. Capture probability (p_i) was modelled as constant, varying through time, varying between groups or both time- and group-variant.

Model averaging

Because of model selection uncertainty, the estimated parameters of all the successfully fitted models were averaged according to their model's AIC_c weight. Thus, only models with an AIC_c weight higher than zero contribute to the averaged estimates. These calculations were carried out with the "Model Averaging" function included in MARK. This was done separately for real (φ , p , p_{ent} , N) and derived parameters (N_i).

Spatial activity

To represent the spatial activity range within years (d_1), distances between the two capture points farthest apart were determined for each individual and calculated with ArcMap, for every individual captured at least two times within each respective year. If an individual was captured two or more times in multiple years, the resulting distances were averaged to create the d_1 -value.

Movement distances across one-year intervals (d_2), from 2010 to 2011 and from 2011 to 2012, were calculated. Distances were only calculated if an individual was found at least one time in each of the two years, involved in the interval. If an individual was only captured once within a year, this capture point was used for distance calculation. Capture points of an individual that was captured two or more times within a year, were averaged using ArcMap's "Mean Center" function. The resulting averaged point was then used for distance calculation. Distances were calculated within ArcMap. If an individual was captured in all three years, the two resulting distances were averaged to create the d_2 -value.

Distances across the two-year interval (d_3), from 2010 to 2012, were only calculated if an individual was captured at least one time in each of those years. The calculations happened in the same manner as they were done for the d_2 -values.

The area size of the Minimum Convex Polygons (MCPs) was calculated using ArcMap.

Mann-Whitney U tests (two-tailed) were conducted for d_1 -, d_2 - and d_3 -values and MCP sizes to test for significant differences between the sexes. For this analysis no differentiation was made between d_1 -values from different years or d_2 -values from different intervals. d_3 -values were only compared for Neuwaldegg, as only one female was recaptured in Maurer Wald over the two-year interval. Distances from one-year intervals and two-year intervals were tested for significant differences. For this test, distances of male and female individuals were pooled, except for the d_3 -values from Maurer Wald, for which it was not possible to test for differences between the sexes. In this case, only data from male individuals were used to prevent the pooling of groups that were not tested for significant differences.

Results

Capture data

Neuwaldegg

Over the three years, the total number of capture events was 806 in Neuwaldegg (Figure 4). Among them, 605 individual animals were identified, 217 were classified as female and 246 as male. The sex of the remaining 142 individuals could not be identified. Capture events were relatively evenly distributed over the three years, 272 in 2010, 257 in 2011 and 277 in 2012.

Total individual recapture rate within years (r_1) was consistent across years. It was lowest in 2011 (9.01 %) and highest in 2012 (11.34 %). Females showed the highest fluctuation with 15.38 % in 2010 and 8.43 % in 2012 (Table 2).

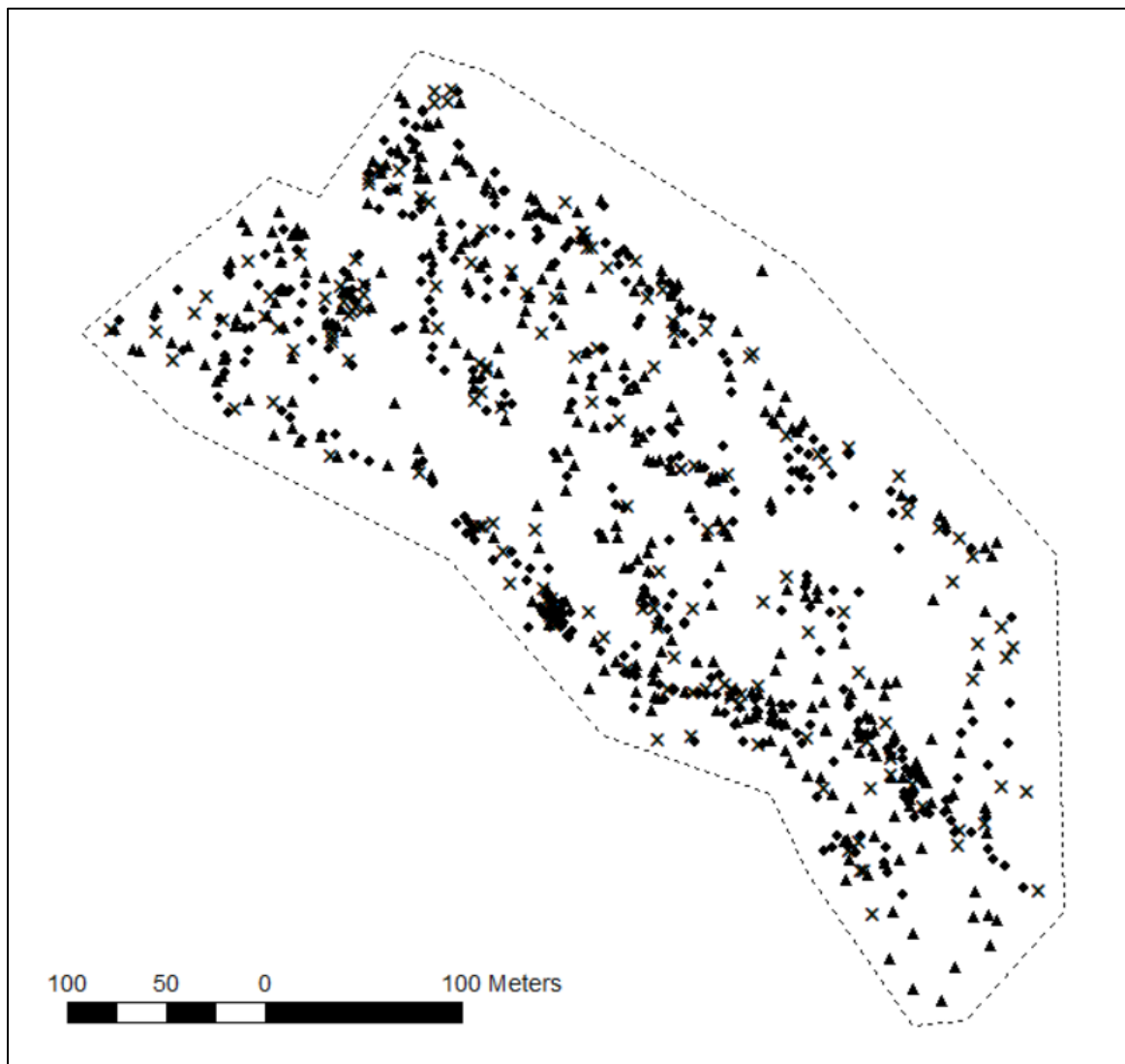


Figure 4: All capture events from Neuwaldegg (2010 to 2012). Different symbols are used for females (triangle), males (filled circle) and unsexed animals (cross). The full line shows the approximate course of the creek and the dotted line the border of the sampling site.

Total individual recapture rates between one-year-intervals (r_2) and the two-year-interval (r_3) were higher than within years (r_1). Whereas the two r_2 -values were almost identical (ca. 16.3 %), r_3 was still higher (20.4 %). Females had lower r_2 -values than males, but a higher r_3 -value (Table 3). In general, the difference between males' r_2 - and r_3 -values were smaller. The differences for males reached values of 1.64 % and 1.94 %, whereas for females they reached values of 6.59 % and 7.60 % (Table 3).

Over the three years 347 (74.95 %) of the sexed individuals were only captured once, 81 (17.49 %) twice and 35 individuals (7.56 %) were caught three or more times. The proportion of singletons, doubletons and individuals captured three or more times was very similar between sexes (Figure 6).

Maurer Wald

The number of capture events during the total sampling period was 321 in Maurer Wald (Figure 5). They were identified as 218 individual animals, 67 females and 116 males. The sex of 35 individuals could not be determined. In 2010, there were 37 capture events, 88 in 2011 and 196 in 2012.

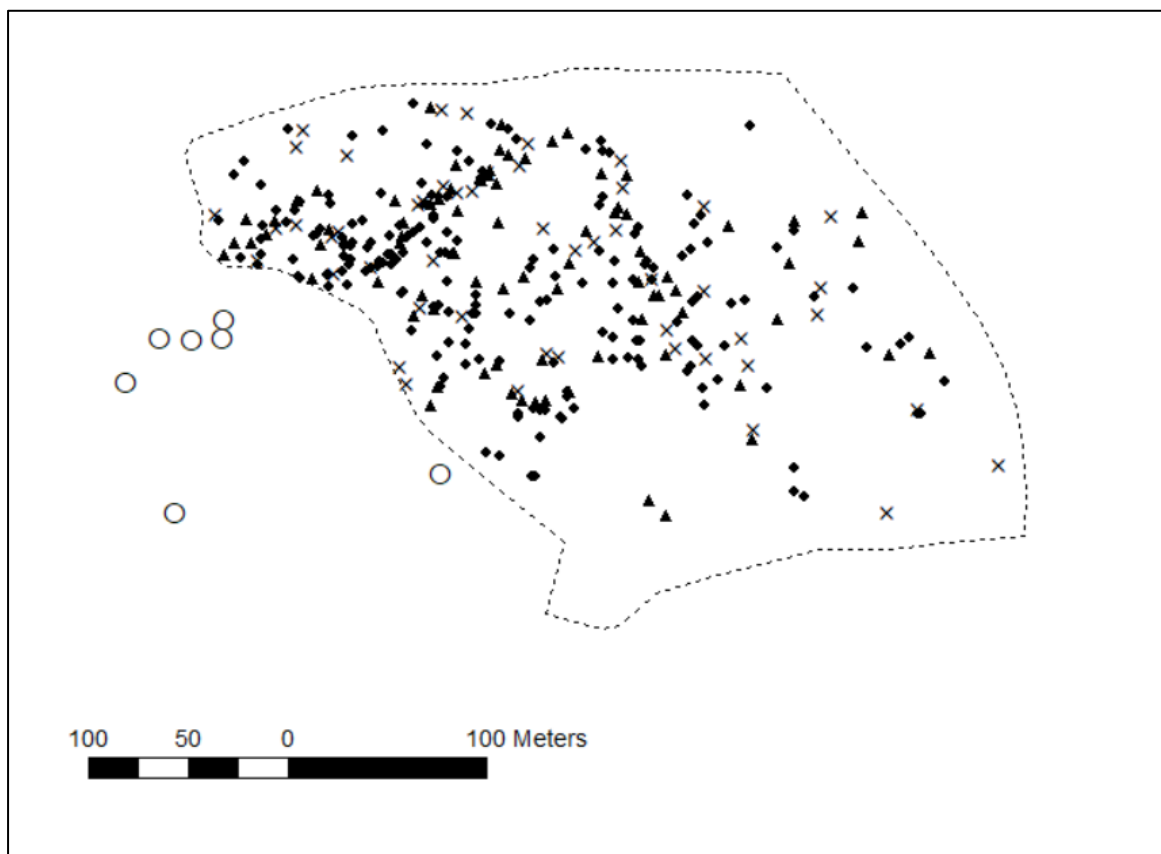


Figure 5: All capture events from Maurer Wald (2010 to 2012). Different symbols are used for females (triangle), males (filled circle) and unsexed animals (cross). Breeding ponds are symbolized by empty circles and the dotted line shows the border of the sampling site.

The r_1 of 2010 was considerably lower than the r_1 of the two following years, in total and both groups. For 2010, total r_1 was 8.82 %, whereas for 2011 and 2012 it had values of 16.22 % and 20.51 %, respectively. Discrepancy between groups was high. Females' r_1 -values ranged from 0 % to 7.69 %, whereas for males they ranged from 12.50 % to 30.23 % (Table 2).

Like in Neuwaldegg, r_2 - and r_3 -values were, in general, considerably higher than r_1 -values. Females' r_2 -values were 20.00 % and 30.77 %, whereas males reached 33.33 % and 45.95 %. Unlike in Neuwaldegg, females' r_3 -value (10 %) was considerably lower than males' (41.67 %) (Table 3).

Of the sexed individuals 119 (65.03 %) were caught once, 46 (25.14 %) twice and 18 (9.84 %) individuals were caught three or more times. The percentage of female singletons was over 20 % higher than of male singletons. Males had a higher number of doubletons and individuals captured three or more times (Figure 6).

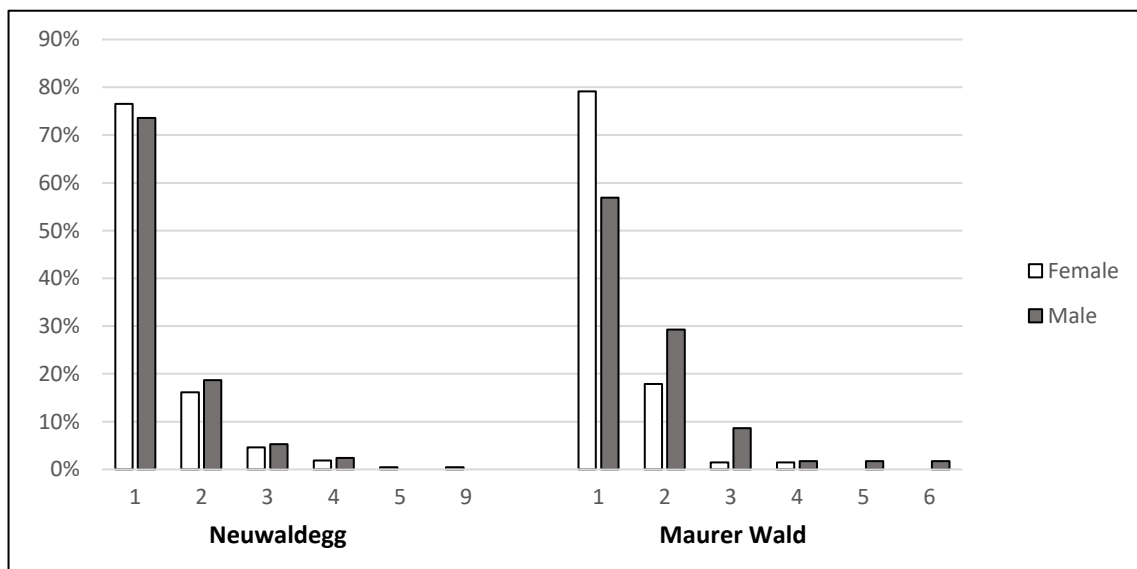


Figure 6: Relative distribution of how often individuals were captured throughout all sampling periods (2010 - 2012) in the respective sampling sites. The percentage on the y-axis corresponds to the total number of sexed individuals captured at each sampling site. Values for females and males are shown separately.

Comparison

Sexual differences between r_1 -values were higher in the data from Maurer Wald. Female r_1 -values from Maurer Wald were lower in 2010 than in the other two years, where they were very similar. Male r_1 -values between sampling sites were on a similar level in 2010 and more than twice as high for Maurer Wald in the other two years. Male r_2 - and r_3 -values from the Maurer Wald data set were about twice as high as the values from Neuwaldegg. For females this trend was only observable for the interval from 2011 to 2012, the r_2 from 2010 to 2011 was similar and the r_3 lower.

Table 2: Individual recapture rates (absolute and relative) within each year of the study. Figures for the total number of individuals, females (F) and males (M), from both sampling sites, are provided separately.

Year	Group	Neuwaldegg			Maurer Wald		
		M	m_1	r_1	M	m_1	r_1
2010	Total	239	25	10.46%	34	3	8.82%
	F	91	14	15.38%	10	0	0.00%
	M	103	9	8.74%	24	3	12.50%
2011	Total	233	21	9.01%	74	12	16.22%
	F	84	8	9.52%	26	2	7.69%
	M	96	11	11.46%	37	10	27.03%
2012	Total	247	28	11.34%	156	32	20.51%
	F	83	7	8.43%	42	3	7.14%
	M	100	13	13.00%	86	26	30.23%

M refers to the number of individuals captured and released during the respective year. m_1 denotes the number of individuals, that were caught two or more times during the same year. r_1 denotes the individual recapture rate within years, it is calculated as $r_1 = m_1 / M$.

Table 3: Overview over the individual recapture rates (absolute and relative) between years, for the total number of individuals (Total), females (F) and males (M) separate. Data from both sampling sites are included.

Interval	Group	Neuwaldegg			Maurer Wald		
		M	m_2	r_2	M	m_2	r_2
2010 to 2011	Total	239	39	16.32%	34	10	29.41%
	F	91	15	16.48%	10	2	20.00%
	M	103	19	18.45%	24	8	37.93%
2011 to 2012	Total	233	38	16.31%	74	29	39.19%
	F	84	13	15.48%	26	8	30.77%
	M	96	18	18.75%	37	17	45.95%
		M	m_3	r_3	M	m_3	r_3
2010 to 2012	Total	239	49	20.50%	34	11	32.35%
	F	91	21	23.08%	10	1	10.00%
	M	103	21	20.39%	24	10	41.67%

M refers to the number of individuals captured and released during the former of the two years compared. $m_{2,3}$ denotes the number of individuals, that were released in the former and recaptured in the latter of the two years compared. r_2 denotes the individual recapture rate between one-year intervals and r_3 for the two-year interval. They are calculated as $r_{2,3} = m_{2,3} / M$.

Demographic estimations

The best supported models (CJS and POPAN) for both sampling sites were models with time-independent apparent survival and time-dependent recapture probability. Two CJS models and four POPAN models had a high enough support to be included into the averaged parameter estimations. The data from both sample sites supported the same models, although the POPAN models were ranked differently in each data set. These models differed from each other only by whether φ_i and N were modelled as group-dependent or not. Group-dependency in general had relatively little effect on the model's support (Table 4).

Table 4: Overview of the best supported CJS and POPAN models for the fire salamander populations from both sample sites, Neuwaldegg (NE) and Maurer Wald (MW).

Model structure	Sample site	Model	ΔAICc	w_i	K	Deviance
CJS	NE	$\varphi_{\cdot}, p_t$	0.00	0.710	47	871.84
		φ_g, p_t	1.79	0.290	48	871.28
	MW	$\varphi_{\cdot}, p_t$	0.00	0.742	34	397.08
		φ_g, p_t	2.11	0.258	33	401.79
POPAN	NE	$\varphi_{\cdot}, p_t, N_{\cdot}$	0.00	0.650	54	-1700.73
		$\varphi_g, p_t, N_{\cdot}$	3.15	0.140	56	-1702.40
		φ_g, p_t, N_g	3.50	0.110	56	-1702.04
		$\varphi_{\cdot}, p_t, N_g$	3.73	0.100	56	-1701.81
	MW	$\varphi_g, p_t, N_{\cdot}$	0.00	0.668	41	-410.65
		φ_g, p_t, N_g	2.60	0.183	42	-410.83
		$\varphi_{\cdot}, p_t, N_g$	3.03	0.147	41	-407.63
		$\varphi_{\cdot}, p_t, N_{\cdot}$	11.86	0.002	42	-401.57

Model labels consist of the involved parameters and their dependencies as subscripts. These parameters are apparent survival (φ), recapture probability (p) and super population size (N). Their subscripts designate the parameters as either constant ($\cdot$), time-dependent (t ; different at each capture occasion) or group-dependent (g ; different values for each sex). The probability of entry (p_{ent}) was always modelled in the same manner (time-dependent) and therefore not included in the label. The rest of the table entries are the difference in AICc value between the respective model and the best supported model (ΔAICc), the AICc weight (w_i), the number of estimated parameters (K) and the models deviance. Models were fitted for each model structure and sample site separately.

Apparent survival

Model averaged estimates for monthly apparent survival (φ_m) between sampling sites and groups were consistent except for females from Maurer Wald. While the CJS model estimates for three of four groups had a relatively narrow range of 0.987 to 0.989, for the fourth group (Females from Maurer Wald), φ_m was estimated to be only 0.960. These estimates translate to annual apparent survival (φ_a) of 0.851 to 0.876 and 0.610, respectively. Estimates from the POPAN models were generally a little lower but showed a similar pattern (Table 5).

Table 5: Model averaged estimates for monthly apparent survival (φ_m) and initial population size (N) of females (F) and males (M) of the fire salamander populations from both sample sites, Neuwaldegg (NE) and Maurer Wald (MW). Annual apparent survival (φ_a) is calculated as φ_m^{12} . φ_m is estimated using both CJS and POPAN models; N cannot be estimated using the CJS structure.

Site	Sex	Model structure	φ_m				φ_a	N			
			Est.	SE	LCI	UCI		Est.	SE	LCI	UCI
NE	F	CJS	0.987	0.010	0.945	0.997	0.851	-	-	-	-
		POPAN	0.984	0.009	0.951	0.995	0.827	518	47.43	425.45	611.39
	M	CJS	0.989	0.009	0.943	0.998	0.876	-	-	-	-
		POPAN	0.986	0.009	0.952	0.996	0.844	530	50.43	430.04	628.35
MW	F	CJS	0.960	0.022	0.886	0.986	0.610	-	-	-	-
		POPAN	0.955	0.020	0.896	0.982	0.579	141	18.93	104.05	178.25
	M	CJS	0.989	0.010	0.928	0.998	0.876	-	-	-	-
		POPAN	0.988	0.010	0.941	0.998	0.862	165	35.29	96.36	234.69

Recapture probability

The recapture probability parameters were always modelled as only time-dependent. Therefore, the model averaged estimates were the same for both groups but were different for each capture occasion. The estimates strongly differed between capture occasions and correlated to the number of animals captured on the respective occasions in both CJS and POPAN models. Up to the eleventh capture occasion the confidence intervals for these estimates were quite large and therefore the estimates yield no meaningful results. They were excluded from further analysis and discussion. The CJS models yielded no estimates for the occasions 34, 35 and 44 for the Neuwaldegg data set and for occasions 12, 13, 17, 20, 23, 29 and 33 for the Maurer Wald data set. For the Neuwaldegg data set, the estimates ranged from 0.003 to 0.077 for CJS and from 0.001 to 0.086 for POPAN models, whereas they ranged from 0.006 to 0.221 for CJS and from 0.004 to 0.234 for POPAN models for the Maurer Wald data set (Attachment: Figures 13-16).

Table 6: Model averaged estimates for annual recapture probability (p_a) for females (F) and males (M) from both sample sites. The CJS model structure was used.

Year	Sex	Neuwaldegg			Maurer Wald		
		Estimate	LCI	UCI	Estimate	LCI	UCI
2011	F	0.172	0.131	0.223	0.416	0.217	0.647
	M	0.179	0.138	0.229	0.421	0.244	0.621
2012	F	0.172	0.133	0.219	0.451	0.231	0.692
	M	0.179	0.141	0.224	0.454	0.254	0.670

The estimates for annual recapture probabilities (p_a) for Maurer Wald were more than twice as high as the estimates for Neuwaldegg for both sexes (Table 6). They ranged from 0.172 to 0.179 for Neuwaldegg and from 0.416 to 0.454 for Maurer Wald. Differences between years and sexes were low.

Population size (N , N_i) and density

Both the super population size (N) and the net population sizes (N_i) for each capture occasion were estimated using the POPAN model structure. Model averaging yielded super population estimates of 518 females and 530 males for the sampling site in Neuwaldegg. For Maurer Wald 141 females and 165 males were estimated.

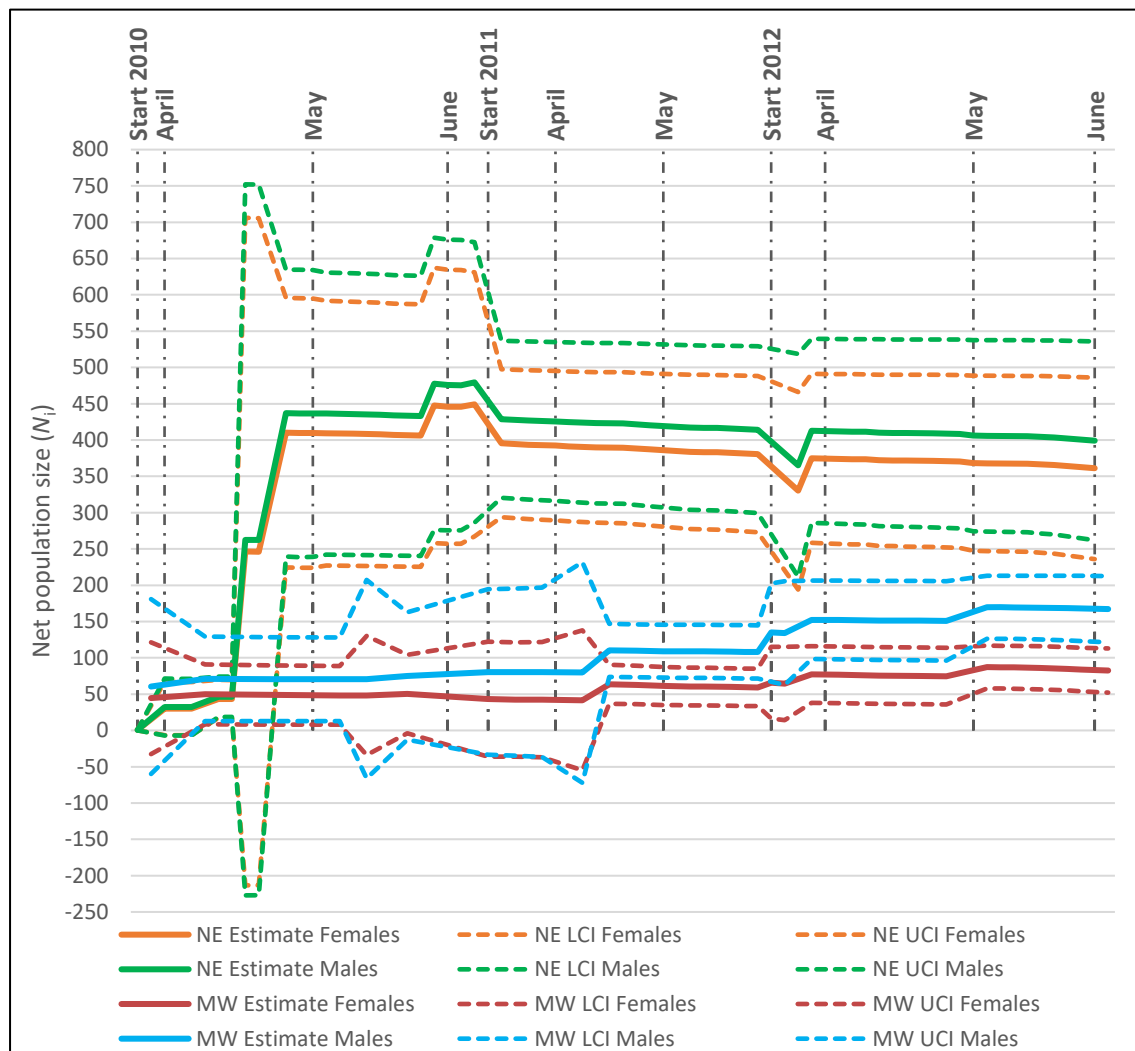


Figure 7: Net population sizes (N_i) for each capture occasion i . Separate graphs are provided for Neuwaldegg (NE) and Maurer Wald (MW) and sexes respectively. Dashed lines denote the lower (LCI) and upper (UCI) bound of the estimates 95%-CI, corresponding to the same color. Dashed vertical lines denote the first capture occasion (CO) of a year or the first CO of a month of the priorly stated year.

Net population size estimates (N_i) for Neuwaldegg were only reliable from the ninth capture occasion (28.04.2010) onwards. The estimates for earlier occasions were unrealistic compared to the rest of the estimates. The large 95 % CI range made the

estimates highly uncertain and therefore they were removed from further analysis and discussion. Estimates for the rest of the occasions were rather stable, for both sexes. The estimated value slightly decreased over time. The occasion on 27.03.2012 yielded the lowest estimates with sizes of 330 (44 ind/ha; females) and 365 (48 ind/ha; males) individuals, whereas the highest estimates were calculated for 07.06.2010 with values of 449 (60 ind/ha; females) and 479 (64 ind/ha; males), respectively. Just as for the super population size, the estimates for net population size were considerably lower for Maurer Wald. The estimates steadily increased over time. For females, the lowest estimate (42; 8 ind/ha) was calculated for 12.04.2011 and the highest (87; 18 ind/ha) for 04.05.2012. Males had the lowest estimated population size (71; 14 ind/ha) on 03.05.2010, whereas the highest value (169; 34 ind/ha) was reached on 04.05.2012. The estimates showed no recurring patterns over the annual sampling periods (Figure 7).

Spatial activity

The annual maximum movement distances (d_1 ; Figure 8) of females (median: 23.9 m) and males (median: 24.1 m) from Neuwaldegg showed no significant differences (Table 7). The largest observed d_1 occurred in 2012 with a distance of 224 m. Only three d_1 -values exceeded the mark of 100 m. Of the nine highest (~15 %) movement distances within years (d_1) across all three years, seven were covered by females and two by males. These numbers translate to 25.93 % and 6.06 % of each group's total number of d_1 -values, respectively. Also, for Maurer Wald the d_1 -values (Figure 8) showed no significant differences (Table 7) between females (median: 33.10 m) and males (median: 31.81 m). None exceeded a distance of 100 m. Of the six highest (~15 %) movement distances within years (d_1) across all three years, one was covered by a female and five by males. This translates to 20.0 % and 13.89 % of each group's total number of d_1 -values, respectively. In Maurer Wald sample sizes for females' d_1 -values were small for all three years ($n < 3$).

Results for d_2 -values (Figure 9) showed a similar pattern. Comparisons between sexes, in Neuwaldegg and Maurer Wald, showed no significant differences (Table 7). In Neuwaldegg four d_2 -values exceeded the mark of 100 m. Of the eight highest (~15 %)

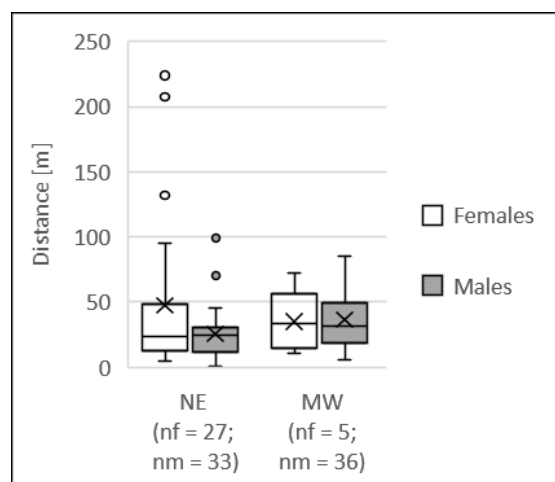


Figure 8: d_1 -values presented for each sample site (NE $\triangleq$ Neuwaldegg; MW $\triangleq$ Maurer Wald) and sex separately. Crosses symbolize the mean and horizontal lines within the boxes the median values. The box lies between the lower quartile (25th percentile) and the upper quartile (75th percentile). Whiskers denote the minimum and maximum values, not counting outliers. Outliers are values that are more than 1.5*IQR higher than the upper or less than the lower quartile and are denoted as circles. Sample sizes for females (nf) and males (nm) are provided.

distances across one-year intervals (d_2) from Neuwaldegg, three were covered by female and five by male individuals. These numbers translate to 15.00 % and 15.63 % of each group's total number of d_2 -values, respectively. Of the five highest (~15 %) distances across one-year intervals (d_2) from Maurer Wald two were covered by females and three by males, which were 20.00 % and 14.29 % of their group's total number of d_2 -values. None of the d_2 -values from Maurer Wald exceeded the 100 m mark.

Differences in sexes regarding the d_3 -values (Figure 10) could only be tested for Neuwaldegg. The results showed no significant differences (Table 7). Only one value from Maurer Wald and none from Neuwaldegg exceeded 100 m. Of the six highest distances across two-year intervals (d_3), three were covered by each, females and males, respectively, which for both groups was corresponding to 14.29 % of their d_3 -values. The comparison of d_2 - and d_3 -values (Figure 11) from each sample site, respectively, showed no significant differences (Table 7).

Median values of the Minimum Convex Polygon (MCP) sizes for Neuwaldegg were 113.4 m² (females) and 132.7 m² (males). For Maurer Wald, they were 87.1 m² (females) and 136.0 m² (males). The percentage of total MCP sizes smaller than 500 m² was 86.1 % for Neuwaldegg and 75.0 % for Maurer Wald (Figure 12). The test for differences between sexes yielded no significant results for Neuwaldegg ($U=154$; $p=0.849$). For Maurer Wald, due to the female's small sample size ($nf = 2$) it was not possible to test MCP size for significance.

Figures 17 and 18 (Attachment) show visualizations of movement areas and distances.

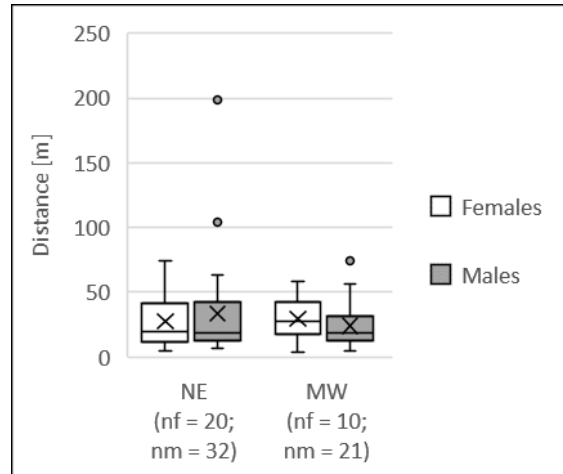


Figure 9: d_2 -values presented for each sample site (NE $\triangleq$ Neuwaldegg; MW $\triangleq$ Maurer Wald) and sex separately. Crosses symbolize the mean and horizontal lines within the boxes the median values. The box lies between the lower quartile (25th percentile) and the upper quartile (75th percentile). Whiskers denote the minimum and maximum values, not counting outliers. Outliers are values that are more than 1.5*IQR higher than the upper or less than the lower quartile and are denoted as circles. Sample sizes for females (nf) and males (nm) are provided.

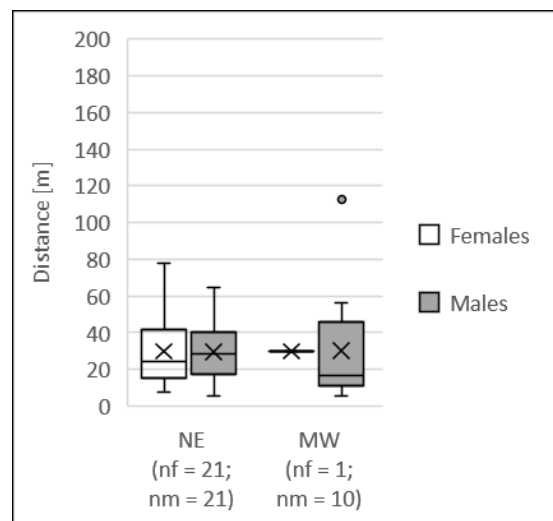


Figure 10: d_3 -values presented for each sex, from each sample site (NE $\triangleq$ Neuwaldegg; MW $\triangleq$ Maurer Wald). Crosses symbolize the mean and horizontal lines within the boxes, the median values. The box lies between the lower quartile (25th percentile) and the upper quartile (75th percentile). Whiskers denote the minimum and maximum values, not counting outliers. Outliers are values that are more than 1.5*IQR higher than the upper or less than the lower quartile and are denoted as circles. Sample sizes for females (nf) and males (nm) are provided.

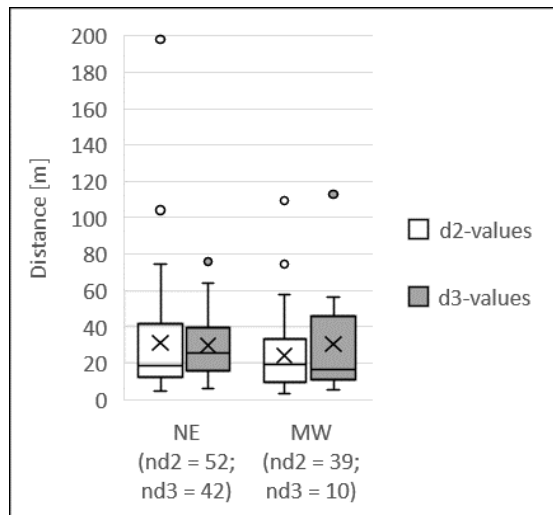


Figure 11: Comparison of the d_2 - and d_3 -values for each sample site (NE $\triangleq$ Neuwaldegg; MW $\triangleq$ Maurer Wald). Values of male and female individuals are pooled, except d_3 -values from Maurer Wald, which consist only of data from males. Crosses symbolize the mean and horizontal lines within the boxes, the median values. The box lies between the lower quartile (25th percentile) and the upper quartile (75th percentile). Whiskers denote the minimum and maximum values, not counting outliers. Outliers are values that are more than 1.5*IQR higher than the upper or less than the lower quartile and are denoted as circles.

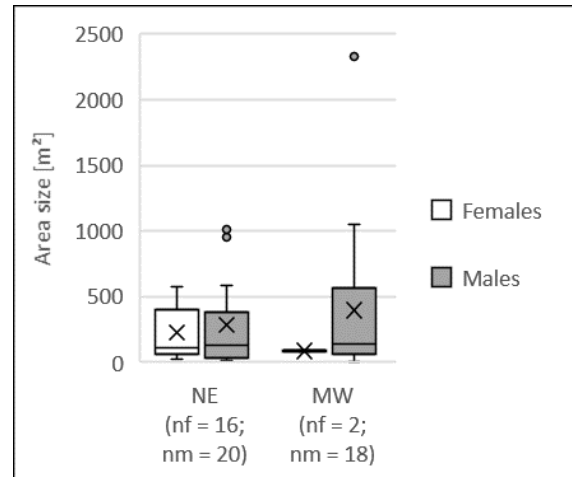


Figure 12: MCP sizes for each sex, from Neuwaldegg (NE) and Maurer Wald (MW). Crosses symbolize the mean and horizontal lines within the boxes, the median values. The box lies between the lower quartile (25th percentile) and the upper quartile (75th percentile). Whiskers denote the minimum

Table 7: Overview of the Mann-Whitney U tests, checking various samples of movement measurements (d_1 , d_2 and d_3) for significant differences. The sample sites Neuwaldegg (NE) and Maurer Wald (MW) as well as the sexes (F, M) used in the samples are stated. Median values movement measurements are provided in meters [m] and MCP sizes in square meters [m²].

Site	Sample A	Sample B	Median A	Median B	U	p
NE	d_1 ; F	d_1 ; M	23.94	24.16	365	0.232
	d_2 ; F	d_2 ; M	19.62	18.84	302	0.735
	d_3 ; F	d_3 ; M	24.56	28.28	204	0.678
	d_2 ; M + F	d_3 ; M + F	18.84	25.64	1006	0.513
	MCP; F	MCP; M	113.40	132.70	154	0.849
MW	d_1 ; F	d_1 ; M	33.10	31.81	85	0.842
	d_2 ; F	d_2 ; M	27.07	18.98	80	0.291
	d_2 ; M + F	d_3 ; M	18.98	16.82	190	0.566

Discussion

Goodness-of-fit testing

Because of a generally low recapture probability, it is possible that the goodness-of-fit test could not detect any sign of detection heterogeneity, although a proportion of the individuals found might not have been continuously present at the sampling area. Several of the following suggestions imply the possibility of individuals temporarily migrating to and from the sampling areas.

Survival and emigration rates

Females from Maurer Wald seemed to have a higher emigration or mortality rate than males, whereas in Neuwaldegg there were no such discrepancies. Possible reasons are varying breeding water conditions or dangers accompanied by the breeding migration.

In Maurer Wald, not only were females captured less often than males, their recapture rates (r_1 , r_2 and r_3) also lay considerably lower than those of males. Such effects were not observed in Neuwaldegg, where recapture rates (r_1 and r_2) were very similar between sexes. The apparent survival estimates followed a similar trend. Monthly (φ_m) and annual (φ_a) apparent survival estimates for both sexes from Neuwaldegg and males from Maurer Wald were rather similar and coincided with the estimates from other studies (Schmidt et al. 2005, Schmidt et al. 2014, Balogová et al. 2017). The estimated φ_a for females from Maurer Wald were considerably lower (Table 5).

The low φ_a of females from Maurer Wald might be explained by an increased mortality rate. Balogová et al. (2017) reported unequal apparent survival (φ) estimates for salamanders wintering in Slovakian caves and attributed this to a higher mortality of females due to their energy demanding migrations to the breeding waters. Furthermore, during the present study, approximately ten cases were observed (own observations; pers. comm. C. Leeb & G. Gollmann) where female fire salamanders had been drowned by male frogs (*Rana* sp.), which were using the same ponds as breeding waters.

Varying migration patterns and destinations of females, caused by annually changing breeding water availabilities in Maurer Wald, might be another reason for the low φ_a . In a study on hibernation activity by Leeb (2013), which took place during the same time period as the present study, no significant differences in the annual return rates to the hibernation site were found between the sexes. This supports the argument in favour of movement activity being the reason for the lower φ_a , while making a higher mortality rate less probable.

Recapture rates and probabilities

In general, the chance of recapturing individuals was higher in Maurer Wald, possibly due to terrain attributes.

When the number of capture events from the two study sites were similar, the r_1 -values from Maurer Wald surpassed the values from Neuwaldegg by far. This falls in line with the model averaged estimates for annual recapture probabilities (p_a). Although generally low, the estimates for Maurer Wald were more than twice as high as the estimates for Neuwaldegg. These values probably were strongly influenced by the sampling sites' terrain. The site in Maurer Wald was flatter, thus more easily observable and provided fewer hiding spots, which probably resulted in a higher detection rate. Balogová et al. (2017) reported similar results for two habitats with unequal observability.

Breeding frequency

A portion of females in Neuwaldegg might skip years in which they reproduce, due to the demanding migration.

In Neuwaldegg the recapture rate of females in the two-year-interval was higher compared to the rates of the one-year intervals. This fluctuation was not confirmed in Maurer Wald. Females of various other long-lived amphibian species occasionally skip years of reproduction because of high reproductive investment or unfavourable environmental conditions (Bull & Shine 1979, Cayuela et al. 2014). Consequently, during these years, they have a reduced probability of being detected. To come to conclusive results in this regard, data over a longer time span would be needed.

Population density

Population density in Neuwaldegg was more than twice as high as in Maurer Wald, which might be due to different environmental conditions. Values might be overestimated due to temporal aggregations during the breeding season.

With sampling area size taken into consideration, the resulting estimation for population density in Neuwaldegg is still more than twice as high as in Maurer Wald. Beech forests with running waters are a common habitat for fire salamanders, whereas habitats with temporary pools are more of an exception (Thiesmeier 2004). Although the larvae are able to adapt to these conditions to some degree (Weitere et al. 2004, Schulte 2008, Keckeis 2013) this preference might generally reflect a better suitability of habitats containing running waters. While planktonic prey density is usually lower in streams (Thiesmeier 2004) there is also lower density of salamander larvae and potential predators, which reduces competition and risk of predation. It was shown in other amphibian species that

the number of successfully metamorphosed animals alone can greatly influence population density (Beebee et al. 1996). In streams larvae also have the possibility to drift to another section of the stream if the conditions worsen (Thiesmeier & Schuhmacher 1990).

Environmental differences might also play a major role. Oak-hornbeam forests (Maurer Wald) are usually located at drier locations than beech forests (Neuwaldegg) (Ellenberg 1988). This limits the time the salamanders can spend on the surface feeding and maybe also the available food. In a study carried out in the same sampling areas as the present study (Mayerhofer 2013), captured females from Neuwaldegg had a significantly higher body condition measured by the Scaled Mass Index (Peig & Green 2009).

The rising trend in net population size estimates might signal that the maximum population density, which the habitat in Maurer Wald can support, is not yet reached. There were no reports of occurrence of *S. salamandra* in Maurer Wald at least up until 1988 (Tiedemann 1990). The first documented sightings at this site were from 2006 (Gollmann 2006). Therefore, it is possible that the population, at the time of sampling, was still in the process of establishing. Grillitsch (1990) reported observations of *Hyla arborea* up until 1980 in a pond close to the sampling area. No occurrence of *Hyla arborea* was observed during this study. This implies that those ponds were less shaded in the past, which would have been less favourable for salamander larvae.

Spatial activity

Recapture data

The fact that total recapture rates within years (r_1) were universally lower than total recapture rates between years (r_2, r_3), in both Neuwaldegg and Maurer Wald hints to a seasonal site fidelity in both sampling sites. As the sample areas are both close to the respective breeding waters, this makes sense for the females at least. Manenti et al. (2017) observed that also male fire salamanders move closer to the breeding sites during breeding season, presumably to increase their chances to find a mate. This might increase the population density near the breeding waters without changing the sex ratio.

Movement distances and home ranges

No evidence for differences between the sexes regarding movement patterns or home range size were found. There were also no significant differences between d_2 - and d_3 -values, which would have signalled home ranges shifting in a continuous direction. Calculated home range sizes were within range of values known from literature (Denoël 1996, Catenazzi 1998, Schulte et al. 2007).

Distances within years

Although the farthest distances within years (d_1) seemed to be covered to a larger percentage by female individuals, no significant differences between movement distances

(d_1) of the sexes was found. Most of the recaptured individuals in Neuwaldegg (86.67 %) and Maurer Wald (78.05 %) were observed to move inside of a diameter smaller than 50m within the same year and therefore seem rather sedentary. However, in Kottenforst (West Germany) a considerable proportion of two salamander subpopulations was reported to have covered distances that exceeded the length of the observed areas of the present study by far (Hendrix et al. 2017). Therefore, to acquire conclusive results regarding total movement distances, larger areas need to be sampled.

Distances across years

In regard to sexual differences d_2 - and d_3 -values can be discussed as one, as they show the same effect, only at a different resolution. Both tests did not yield significant results, thus, spatial shifts of the home range did not differ between the sexes. Very similar to the d_1 -values, most of both, d_2 - and d_3 -values from both sample sites, were below the 50m threshold. If there was a shift of the home ranges in a continuous direction, d_3 -values (distances over two years) should be larger than d_2 -values (distances over one year). The results show that this was not the case.

Home ranges

Mean sizes of the Minimum Convex Polygons (MCPs) of males and females showed no differences. Combined (mean $\pm$ SD: $260 \pm 275 \text{ m}^2$) they lie noticeably lower than the home ranges reported by Schulte et al. (2007) (mean $\pm$ SD: $1295 \pm 853 \text{ m}^2$) but at the same time are larger than the results of earlier literature. Denoël (1996) reported mean sizes of 55 m^2 and Catenazzi (1998) sizes ranging from 5 to 255 m^2 . These MCP sizes should be considered minimum home ranges, as many consist only of three capture points. Home range sizes might also strongly vary with the time of the year the sampling was done. For some populations of *S. salamandra* the winter and summer quarters lie at different locations (Feldmann 1987, Thiesmeier 2004). If sampling was done during these migrations, home range estimates should be expected to be larger compared to sampling outside of these times.

Conclusion

The assumption that the population density was lower in Maurer Wald was confirmed. Female salamanders from Maurer Wald might be especially under pressure because of varying breeding water conditions and the risk of being drowned by frogs, indicated by low apparent survival. Emigration rate estimates for the other groups were low, although this site fidelity might only be seasonal. No difference in the movement activity between sexes was found, although sampling areas of larger size would be needed to get conclusive results.

References

- AKAIKE, H. 2011. Akaike's Information Criterion. In: LOVRIC M. (eds) International Encyclopedia of Statistical Science. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-04898-2_110.
- ANDERSON, D. R. & K. P. BURNHAM. 1999. Understanding information criteria for selection among capture-recapture or ring recovery models. *Bird Study* 46: 14-21.
- ARNTZEN, J. W., C. ABRAHAMS, W. R. M. MEILINK, R. IOSIF & A. ZUIDERWIJK. 2017. Amphibian decline, pond loss and reduced population connectivity under agricultural intensification over a 38 year period. *Biodiversity and Conservation* 26: 1411-1430.
- BALOGOVÁ, M., D. JELIĆ, M. KYSELOVÁ, & M. UHRIN. 2017. Subterranean systems provide a suitable overwintering habitat for *Salamandra salamandra*. *International Journal of Speleology* 46: 321-329.
- BALOGOVÁ, M., M. KYSELOVÁ & M. UHRIN. 2016. Changes in dorsal spot pattern in adult *Salamandra salamandra* (LINNAEUS, 1758). *Herpetozoa* 28: 167-171.
- BAR-DAVID, S., O. SEGEV, N. PELEG, N. HILL, A. R. TEMPLETON, C. B. SCHULTZ & L. BLAUSTEIN. 2007. Long-distance movements by fire salamanders (*Salamandra atra*) and implications for habitat fragmentation. *Israel Journal of Ecology and Evolution* 53: 143-159.
- BEEBEE, T. J. C., J. S. DENTON & J. BUCKLEY. 1996. Factors Affecting Population Densities of Adult Natterjack Toads *Bufo calamita* in Britain. *Journal of Applied Ecology* 33: 263-268.
- BOLGER, D.T., T.A. MORRISON, B. VANCE, D. LEE & H. FARID. 2012. A computer-assisted system for photographic mark-recapture analysis. *Methods in Ecology and Evolution* 3: 813-822.
- BONATO, L. & G. FRACASSO. 2003. Movements, distribution pattern and density in a population of *Salamandra atra aurorae* (Caudata: Salamandridae). *Amphibia-Reptilia* 24: 251-260.
- BOWER, D. S., K. R. LIPS, L. SCHWARZKOPF, A. GEORGES & S. CLULOW. 2017. Amphibians on the brink. *Science* 357: 454-455.
- BULL, J.J. & R. SHINE. 1979. Iteroparous animals that skip opportunities for reproduction. *The American Naturalist* 114: 298-303.
- BURNHAM, R. A, G. C. WHITE & D. R. ANDERSON. 1995. Model selection strategy in the analysis of capture-recapture data. *Biometrics* 51: 888-898.
- CABELA, A., H. GRILLITSCH & F. TIEDEMANN. 2001. Atlas zur Verbreitung und Ökologie der Amphibien und Reptilien in Österreich: Auswertung der Herpetofaunistischen

- Datenbank der Herpetologischen Sammlung des Naturhistorischen Museums in Wien. 176-190. Wien: Umweltbundesamt.
- CATENAZZI, A. 1998. Ecologie d'une population de Salamandre tachetée au Sud des Alpes. Diploma thesis at the University of Neuchâtel. Not published.
- CAYUELA, H., A. BESNARD, E. BONNAIRE, H. PERRET, J. RIVOALEN, C. MIAUD & P. JOLY. 2014. To breed or not to breed: Past reproductive status and environmental cues drive current breeding decisions in a long-lived amphibian. *Oecologia* 176: 107.
- CHAO, A. 2001. An overview of closed capture-recapture models. *Journal of Agricultural, Biological, and Environmental Statistics* 6: 158-175.
- CSILLÉRY, K. & S. LENGYEL. 2004. Density dependence in stream-dwelling larvae of fire salamander (*Salamandra salamandra*): A field experiment. *Amphibia-Reptilia* 25: 343-349.
- CUSHMAN, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation* 128: 231-240.
- DENOËL, M. 1996. Phénologie et domaine vital de la salamandre terrestre *Salamandra salamandra terrestris* (Amphibia, Caudata) dans un bois du Pays de Herve (Belgique). *Cathiers d'Ethiologie* 16: 291-306.
- DUELLMAN, W. E. & L. TRUEB. 1994. *Biology of Amphibians*. The John Hopkins University Press. Baltimore & London.
- ELLENBERG, H. H. 1988. *Vegetation ecology of central Europe*. Cambridge University Press.
- FELDMANN, R. 1967. Nachweis der Ortstreue des Feuersalamanders, *Salamandra salamandra terrestris* Lacépède, 1788, gegenüber seinem Winterquartier. *Zoologischer Anzeiger* 178: 42-48.
- FELDMANN, R. 1987. Überwinterung, Ortstreue und Lebensalter des Feuersalamanders, *Salamandra salamandra terrestris*. Schlussbericht einer Langzeituntersuchung. *Jahrbuch für Feldherpetologie* 1: 33-44.
- GIMENEZ, O., E. CAM & J.-M. GAILLARD. 2017. Individual heterogeneity and capture–recapture models: What, why and how? *Oikos* 127: 664-686.
- GOLLMANN, G. 2006. Kartierung der Amphibienvorkommen im Natura 2000-Gebiet Liesing. Projektbericht im Auftrag der Magistratsabteilung 22 – Umweltschutz, Wien.
- GRILLITSCH, H. 1990. Europäischer Laubfrosch. In F. TIEDEMANN (Ed.), *Lurche und Kriechtiere* Wiens: 80-86. J & V Edition Wien.
- GROVER, M. C. 1998. Influence of cover and moisture on abundances of the terrestrial salamanders *Plethodon cinereus* and *Plethodon glutinosus*. *Journal of Herpetology* 32: 489-497.

- HARPER, E. B., T. A. G. RITTENHOUSE & R. D. SEMLITSCH. 2008. Demographic consequences of terrestrial habitat loss for pool-breeding amphibians: Predicting extinction risks associated with inadequate size of buffer zones. *Conservation Biology* 22: 1205-1215.
- HENDRIX, R., B. R. SCHMIDT, M. SCHAUB, E. T. KRAUSE & S. STEINFARTZ. 2017. Differentiation of movement behaviour in an adaptively diverging salamander population. *Molecular Ecology* 26: 6400-6413.
- KECKEIS, S. 2013. Geometric morphometrics of body shape of *Salamandra salamandra* larvae from diverse water bodies. Master's Thesis – University of Vienna. <http://othes.univie.ac.at/29799/>.
- KLEWEN, R. 1985. Untersuchungen zur Ökologie und Populationsbiologie des Feuersalamanders (*Salamandra salamandra terrestris* Lacépède, 1788) an einer isolierten Population im Kreis Paderborn. – Abhandlungen aus dem Landesmuseum für Naturkunde Münster 47: 1-51.
- LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT & D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs* 62: 67-118.
- LEEB, C. 2013. Mass hibernation and notes on winter activity of fire salamanders (*Salamandra salamandra*) in the Maurer Wald (Vienna, Austria). Master's Thesis – University of Vienna.
- LEEB, C., W. HÖDL, & M. RINGLER. 2013. A high-quality, self-assembled camera trapping system for the study of terrestrial poikilotherms tested on the fire salamander. *Herpetozoa* 25: 164-171.
- LUKACS, P. M. & K. P. BURNHAM. 2005. Review of capture-recapture methods applicable to noninvasive genetic sampling. *Molecular Ecology* 14: 3909-3919.
- MARTEL, A., A. SPITZEN-VAN DER SLUIJS, M. BLOOI, W. BERT, R. DUCATELLE, M. C. FISHER, A. WOELTJES, W. BOSMAN, K. CHIERS, F. BOSSUYT & F. PASMANS. 2013. *Batrachochytrium salamandrivorans* sp. nov. causes lethal chytridiomycosis in amphibians. *Proceedings of the National Academy of Sciences of the United States of America* 110: 15325-15329.
- MANENTI, R., G. F. FICETOLA & F. DE BERNARDI. 2009. Water, stream morphology and landscape: Complex habitat determinants for the fire salamander *Salamandra salamandra*. *Amphibia-Reptilia* 30: 7-15.
- MANENTI, R., A. CONTI & R. PENNATI. 2017. Fire salamander (*Salamandra salamandra*) males' activity during breeding season: Effects of microhabitat features and body size. *Acta Herpetologica*, 12: 29-36.
- MARVIN, G. A. 2001. Age, growth, and long-term site fidelity in the terrestrial plethodontid salamander *Plethodon kentucki*. *Copeia* 2001: 108-117.

- MAYERHOFER, M. 2013. Life-history variation in fire salamanders (*Salamandra salamandra*, LINNAEUS, 1758) in the Vienna woods. Master's Thesis – University of Vienna. <http://othes.univie.ac.at/30801/>.
- NÖLLERT, A. & C. NÖLLERT. 1992. Die Amphibien Europas. p. 175. Franckh-Kosmos Verlag-GmbH & Co. KG, Stuttgart.
- PEIG, J., & A. J. GREEN. 2009. New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. *Oikos* 118: 1883-1891.
- POLLOCK, K. H. 2000. Capture-recapture models. *Journal of the American Statistical Association* 95: 295-296.
- POWELL, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65-110 in L. BOITANI & T. FULLER, editors. *Research techniques in animal ecology: Controversies and consequences*. Columbia University Press, New York, New York, USA.
- REBELO, R. & M. H. LECLAIR. 2003. Site tenacity in the terrestrial salamandrid *Salamandra salamandra*. *Journal of Herpetology* 37: 440-445.
- RODGERS, A.R., J.G. KIE, D. WRIGHT, H.L. BEYER & A.P. CARR. 2015. HRT: Home range tools for ArcGIS. Version 2.0. Ontario Ministry of Natural Resources and Forestry, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.
- SANDERCOCK, B. K. 2006. Estimation of demographic parameters from live-encounter data: A summary review. *The Journal of Wildlife Management* 70: 1504-1520.
- SCHMIDT, B.R., M. SCHAUB & B. R. ANHOLT. 2002. Why you should use capture-recapture methods when estimating survival and breeding probabilities: On bias, temporary emigration, overdispersion and common toads. *Amphibia-Reptilia* 23: 375-388
- SCHMIDT, B.R., R. FELDMANN & M. SCHAUB. 2005. Demographic processes underlying population growth and decline in *Salamandra salamandra*. *Conservation Biology* 19:1149-1156.
- SCHMIDT, B.R., M. SCHAUB & S. STEINFARTZ. 2007. Apparent survival of the salamander *Salamandra salamandra* is low because of high migratory activity. *Frontiers in Zoology* 4:19.
- SCHMIDT, B.R., E. ITIN & M. SCHAUB. 2014. Seasonal and annual survival of the salamander *Salamandra salamandra salamandra*. *Journal of Herpetology* 48: 20-23.
- SCHULTE, U. 2008. Phänotypische Unterschiede bei Feuersalamanderlarven (*Salamandra salamandra terrestris*) in Still- und Fließgewässern im Kottenforst bei Bonn. *Zeitschrift für Feldherpetologie* 15: 15-22.

- SCHULTE, U., D. KÜSTERS & S. STEINFARTZ. 2007. A PIT tag based analysis of annual movement patterns of adult fire salamanders (*Salamandra salamandra*) in a Middle European habitat. *Amphibia-Reptilia* 28: 531-536.
- SCHWARZ, C. J. & A. N. ARNASON. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics* 52: 860-873.
- SHOEMAKER, V. & K. A. NAGY. 1977. Osmoregulation in amphibians and reptiles. *Annual Review of Physiology* 39: 449-471.
- SPIGHT, T. M. 1967. The water economy of salamanders: Exchange of water with the soil. *The Biological Bulletin* 132: 126-132.
- SPIITZEN-VAN DER SLUIJS A., A. MARTEL, J. ASSELBERGHS, E. K. BALES, W. BEUKEMA, M. C. BLETZ, L. DALBECK, E. GOVERSE, A. KERRES, T. KINET, K. KIRST, A. LAUDELOUT, L. F. MARIN DA FONTE, A. NÖLLERT, D. OHLHOFF, J. SABINO-PINTO, B. R. SCHMIDT, J. SPEYBROECK, F. SPIKMANS, S. STEINFARTZ, M. VEITH, M. VENCES, N. WAGNER, F. PASMANS & S. LÖTTERS. 2016. Expanding distribution of lethal amphibian fungus *Batrachochytrium salamandrivorans* in Europe. *Emerging Infectious Diseases* 22: 1286-1288.
- THIESMEIER, B. 2004. *Der Feuersalamander*. Laurenti-Verlag, Bielefeld.
- THIESMEIER, B. & H. SCHUHMACHER. 1990. Causes of larval drift of the fire salamander, *Salamandra salamandra terrestris*, and its effects on population dynamics. *Oecologia* 82: 259-263.
- TIEDEMANN, F. (Ed.). 1990. *Lurche und Kriechtiere Wiens*. J & V Edition Wien.
- WEITERE, M., D. TAUTZ, D. NEUMANN, & S. STEINFARTZ. 2004. Adaptive divergence vs. environmental plasticity: Tracing local genetic adaptation of metamorphosis traits in salamanders. *Molecular Ecology* 13: 1665-1677.
- WHITE, G. C. & K. P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46: 120-138.

Attachments

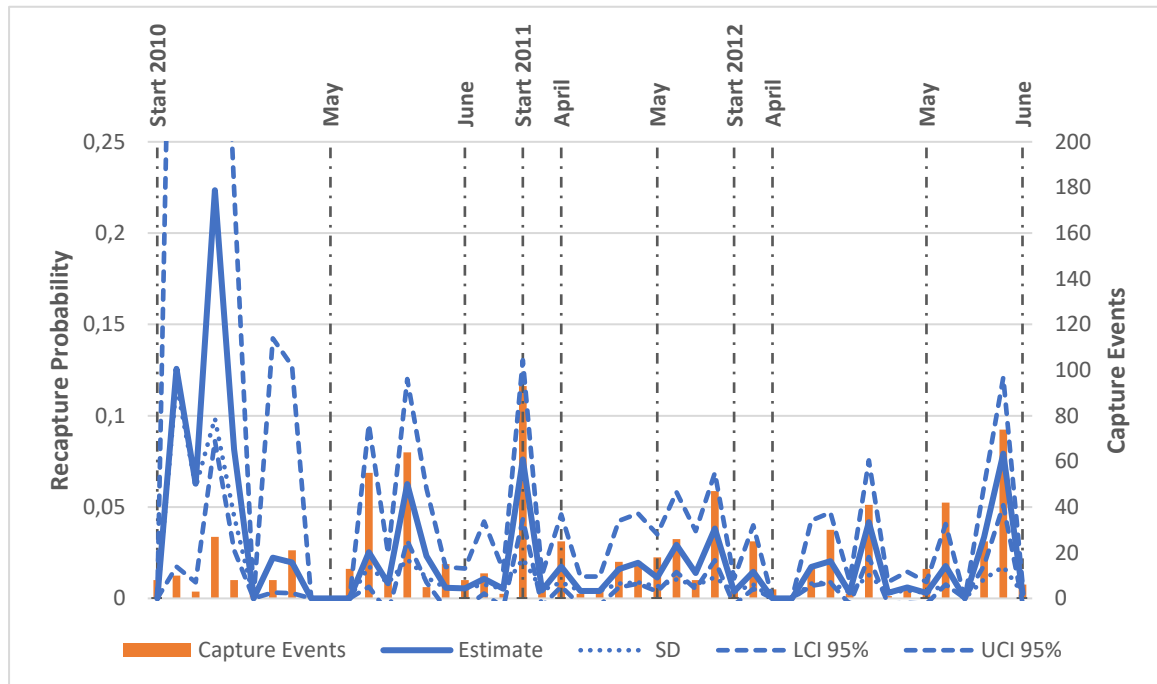


Figure 13: CJS model estimates of the recapture probabilities (p_i) in relation to the number of capture events for the Neuwaldegg sample site. Dashed vertical lines denote the first capture occasion (CO) of a year or the first CO of a month of the prior year.

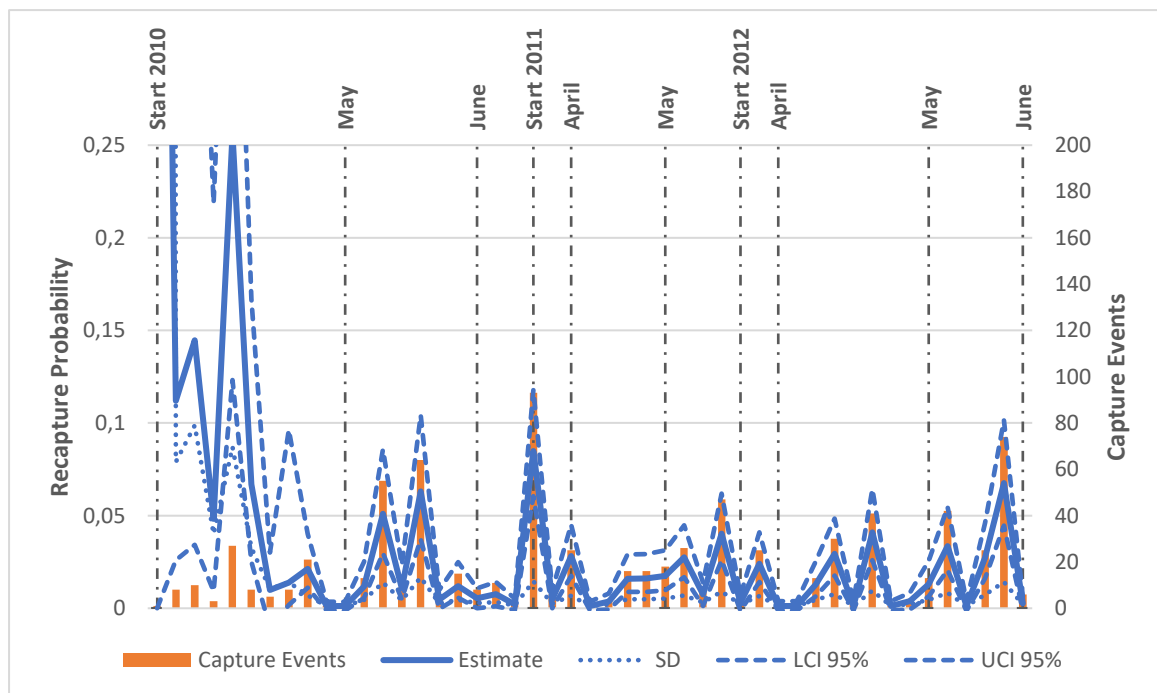


Figure 14: POPAN model estimates of the recapture probabilities (p_i) in relation to the number of capture events for the Neuwaldegg sample site. Dashed vertical lines denote the first capture occasion (CO) of a year or the first CO of a month of the prior year.

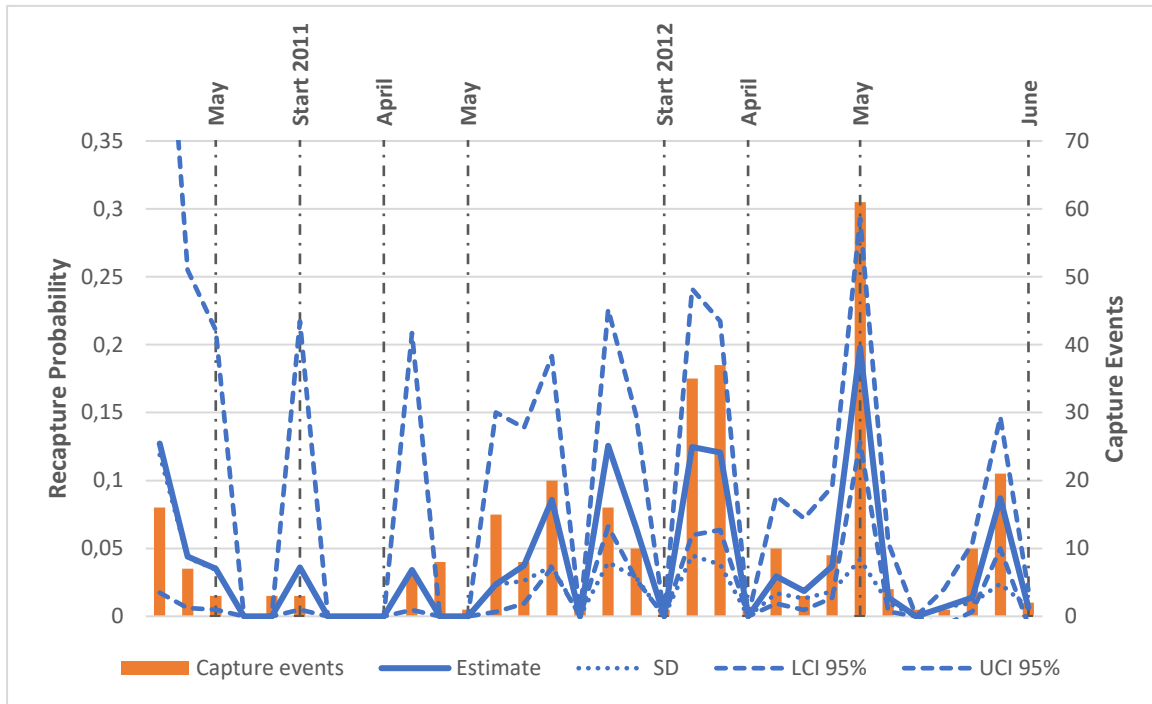


Figure 15: CJS model estimates of the recapture probabilities (p_i) in relation to the number of capture events for the Maurer Wald sample site. Dashed vertical lines denote the first capture occasion (CO) of a year or the first CO of a month of the priorly stated year.

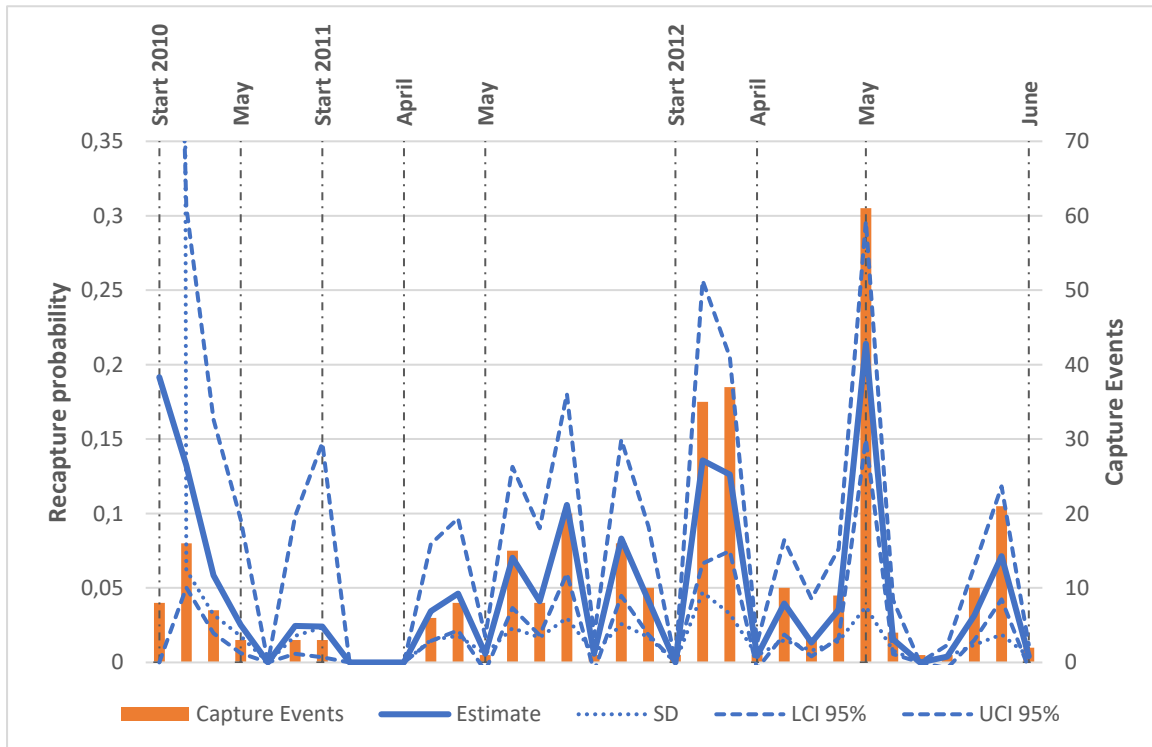


Figure 16: POPAN model estimates of the recapture probabilities (p_i) in relation to the number of capture events for the Maurer Wald sample site. Dashed vertical lines denote the first capture occasion (CO) of a year or the first CO of a month of the priorly stated year.

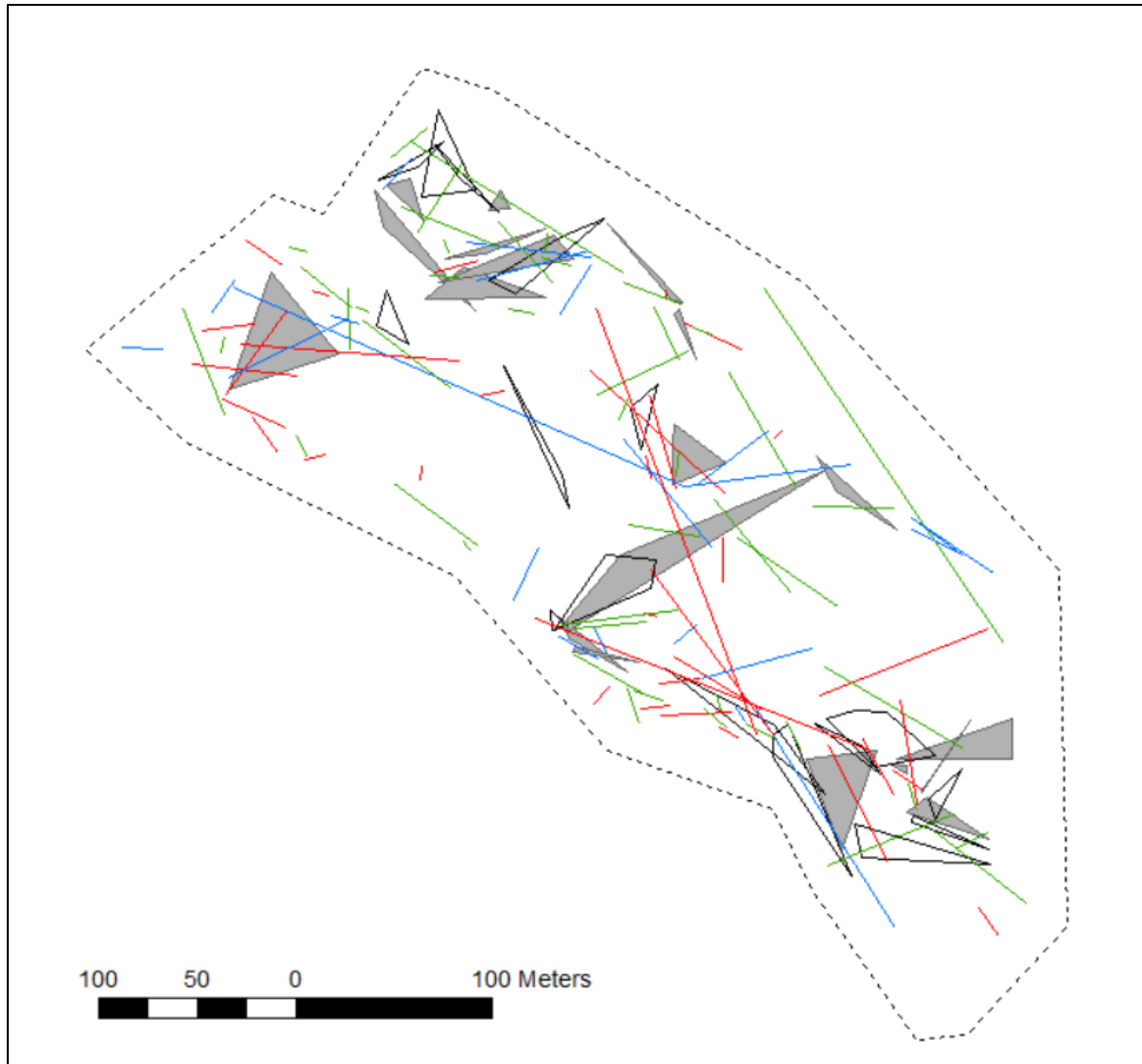


Figure 17: Visualization of area and distances of the individuals' movements over all sample periods in NE. The activity of individuals, captured three times or more, is represented by the means of MCPs (Females: transparent; Males: light grey). Distances between capture locations of individuals recaptured only once are represented by colored straight lines (Females: red; Males: green; Unsexed: blue).

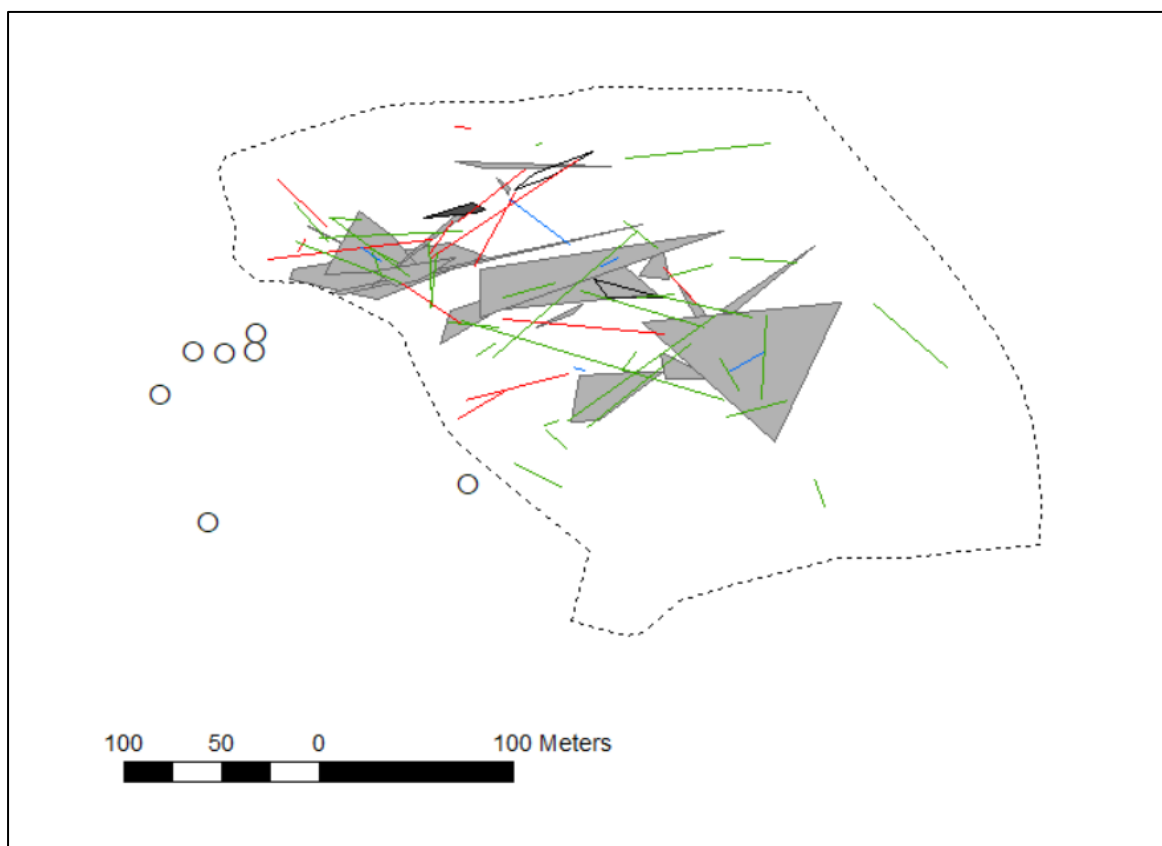


Figure 18: Visualization of area and distances of the individuals' movements over all sample periods in MW. The activity of individuals, captured three times or more, is represented by the means of MCPs (Females: transparent; Males: light grey; Unsexed: dark grey). Distances between capture locations of individuals recaptured only once are represented by straight lines (Females: red; Males: green; Unsexed: blue). Circles denote breeding ponds.

Zusammenfassung

Um den Schutz von Amphibien zu unterstützen, ist es unumgänglich, dass man ihre Populationsdynamik versteht. Neue Daten zur Migrationsaktivität und Ortstreue von *Salamandra salamandra*, aber speziell die Anpassungen dieser Spezies an unterschiedliche Habitate, führten zu viel Diskussion. Diese Fang-Wiederfang-Studie verglich die Strukturen zweier Populationen von *S. salamandra*, welche in verschiedenartigen Habitaten vorkommen. Die Habitate unterscheiden sich hinsichtlich der Feuchtigkeit, der Art der Larvengewässer, der Anzahl der umschließenden Barrieren und ihrer topografischen Eigenschaften. Salamander wurden gefangen, fotografiert und anschließend wieder frei gelassen. Unter Benutzung des Programms MARK wurden, mit Hilfe der Fang-Wiederfang-Daten, demografische Parameter geschätzt. Die Fundorte wurden mit dem Programm ArcGIS aufgenommen, aus denen Distanzen und Aufenthaltsradien berechnet wurden. Weibchen und Männchen wurden auf Unterschiedlichkeit hinsichtlich der demographischen Parameter und ihrer räumlichen Aktivitäten getestet. Die Populationsdichte im Habitat mit Rotbuchenwald und Fließgewässer war doppelt so hoch wie im Habitat mit Eichen-Hainbuchenwald und temporären Teichen. Die jährliche scheinbare Überlebensrate war größtenteils hoch (~ 0.85). Nur die Schätzungen für die Weibchen aus dem Habitat mit geringer Populationsdichte waren sehr niedrig (~ 0.60), was eine hohe Sterbe- oder Emigrationsrate signalisierte. Bewegungsdistanzen und Aufenthaltsradien zeigten keine signifikanten Unterschiede zwischen den Geschlechtern und waren auch zwischen den beiden Habitaten ähnlich. Bewegungsdistanzen zwischen Zwei-Jahres-Intervallen waren nicht signifikant länger, als zwischen Ein-Jahres-Intervallen, was auf keine Verschiebung des Aufenthaltsareals in eine gleichbleibende Richtung hindeutet.

