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# Survival and degree of transience in the fire salamander (*Salamandra salamandra*) population, the eight-year study

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***Abstract*.—We analyzed the survival, transience, and population dynamics of the fire salamander (*Salamandra salamandra*) in an eight-year capture-recapture study using the Cormack-Jolly-Seber model. This apparently healthy population from Central Bohemia does not currently face any serious anthropogenic threats, and our demographic results could therefore be used to assess the extent of negative effects for other populations facing more serious stressors. We focused on the following parameters: lifespan, survival, recapture estimate, population size and abundance trends, degree of transience and site fidelity vs. tendency to disperse. Depending on the year, mean population size estimates range from 146 to 176 for resident adult males and from 109 to 146 for resident adult females. Males are more likely to be on the surface than females. The mean annual apparent survival probability is 0.80 and 0.70 for males and females, respectively (adult residents and transients combined). The net survival probability is 0.91 and 0.90 for adult resident males and females, respectively. The mean life expectancy after reaching sexual maturity (at three years of age) is 10.6 years for resident males and 9.7 years for resident females in our lowland population. The mean level of transience is 0.13 for males and 0.19 for females. The transient behavior of females is a consequence of their spring migration to the breeding stream and the transient behavior of males reflects their autumn search for females. 89% of the males and 85% of the females moved less than 50 m in one year and 52% of the males and 42% of the females moved less than 15 m. There were many individuals of both sexes who remained in the same, or almost the same place, or returned to exactly the same place, even after 4 years.**

**Keywords.** population dynamics, population demography, urodele amphibians, lifespan, site fidelity, capture-mark-recapture, Cormack-Jolly-Seber model

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## Introduction

In salamanders, adaptations to environmental parameters are often manifested as differences in life history and phenotypic traits between and within populations (Arnzten and van Belkom 2020; Munoz et al. 2016), and the fire salamander (*Salamandra salamandra*) is no exception (e.g., Najbar et al. 2020). This highly adaptable species of caudate amphibian exhibits high variability in life history strategies (e.g., Buckley et al. 2007; Denoël 1996; Velo-Anton and Cordero-Rivera 2017) across its wide range (Sillero et al. 2014; Sparreboom 2014). This fossorial species spends long periods underground during the active season and only a fraction of the population is active on the surface at the same time, even during favourable climatic events (e.g., rainy nights) (Kiss et al. 2021; Thiesmeier 2004). It is impossible to estimate demographic parameters of such a species with potentially low capture probability using classical methods based on direct counts (Schmidt et al. 2002). Demographic studies of long-lived species, such as the fire salamander, based on capture-recapture models overcome this problem by allowing for imperfect detection (Angelini et al. 2010) and providing important insights into population trends and life history parameters such as survival, transience, and longevity

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(Schmidt et al. 2005; Kiss et al. 2021).

Survival is a critical demographic process underlying the dynamics of animal populations (Saether and Bakke 2000), and estimating its probability allows us to better understand the demography of natural populations (Nichols et al. 2000; Schmidt et al. 2005). Survival probabilities in animal populations are often estimated based on capture-recapture study designs (Lebreton et al. 1992; Williams et al. 2002) using Cormack-Jolly-Seber (CJS) models, which estimate survival and recapture probabilities (Connette and Semlitsch 2015). In cases where mortality and permanent emigration are convoluted, the survival probability is referred to as ‚apparent survival‘, which is the probability that an individual survives and remains in the study area (Lebreton et al. 1992; Van Drunen et al. 2020).

Dispersal, i.e. the transience level can strongly influence the dynamics, the distribution and the abundance of local amphibian populations and may be critical for their persistence in fragmented landscapes (Dieckmann et al. 1999; Lowe 2003). Amphibian populations are known for large fluctuations in abundance and dispersal between populations is essential to prevent local extinction (Green 2005). The threat of extinction of a local subpopulation is one of the driving factors promoting the evolution of dispersal (Gandon and Michalakis 2001), but dispersal is costly for the individuals (Hanski 1998) and will only be selected for if individuals gain fitness benefits by leaving the natal habitat and emigrating to another habitat patch (Hendrix et al. 2017; Kun and Scheuring 2006). Dispersal strategies depend on the quality of habitat patches, and dispersal is favoured when natal habitat conditions are uncertain and vary over time (Travis 2001). Dispersal is not favoured under conditions that are temporally stable but spatially heterogeneous (Dieckmann et al. 1999; McPeek and Holt 1992), as individuals may be more successful if they remain in the same location (Hendrix et al. 2017). Tendency to disperse and dispersal strategies may differ between populations of the same species due to different habitat conditions in different geographical areas (Doebeli and Ruxton 1997), and fire salamanders are no exception. While some studies provide evidence for the fact that adult fire salamanders can be highly vagile (e.g., Perret 2003; Schmidt et al. 2007; Schulte et al. 2007; Steinfartz et al. 2007) and can move relatively long distances (e.g., Hendrix et al. 2017), other studies suggest that these salamanders are highly sedentary, show strong site fidelity to small home ranges, and that adult transients are not common in populations (Denoël 1996; Ficetola et al. 2012; Joly 1963; Pough et al. 2001; Rebelo and Leclair 2003; Schmidt et al. 2014; Thiesmeier and Grossenbacher 2004). Strong site fidelity and small home ranges have been shown not only for the closely related *S. atra* (Bonato and Fracasso 2003; Klewen 1991), *S. lanzai* (Riberon and Miaud 2000), but also for the North American mole salamander (Church et al. 2022).

Using data from a eight-year capture-recapture study, we modelled survival, recapture rates, transience levels and life spans of adult fire salamanders (*S. s. salamandra*) using the Cormack-Jolly-Seber model. Long-term capture-recapture data and associated estimation methods are probably the most appropriate methods for this type of research, as detection probabilities are estimated and used to adjust counts (Buckland et al. 2001; Hyde and Simons 2001; Williams et al. 2002). Our research objectives were to (a) estimate the survival probabilities of adult salamanders (i.e., the losses that could result from mortality or emigration), (b) determine the recapture response, (c) determine the degree of transience in the population, and (d) investigate trends in abundance.

The EU Habitats Directive (92/43/EEC) require member states to monitor species and habitats and report on their conservation status. Especially, but not only, in the case of amphibians, the result of such monitoring is all too often the detection of negative trends. In the case of fire salamanders, these trends may even result in regional extinctions due to Chytridiomycosis (e.g., Martel et al. 2013). Our apparently healthy population, with stable or even increasing recruitment of juveniles and semi-adults (Table 1), is not currently facing any serious anthropogenic threats other than accidental killing by infrequent cars and bicycles. Our demographic results could therefore be used to assess the extent of negative effects for other populations facing more serious stressors.

## Material and Methods

### Study area

Our study area is located in Central Bohemia (50°10‘11.4’N, 14°22‘38.8’E, 180 m.a.s.l.) north of Prague. The long-term average temperature is 7.9°C and the annual rainfall is 526 mm/m$^2$. It is a small shady valley with scattered houses and a large proportion of broadleaf forest growing on the steep slopes. At the bottom of the valley there is a small first-order stream, which flows into the nearby Vltava River and serves as a breeding habitat for salamanders. It is equally accessible for salamanders from all parts of our study area. We did not find any common hibernacula in our area, nor any autumn or spring migrations of salamanders to such places. Thus, according to Thiesmeier (2004), there are no separate summer and winter quarters in our study area. The area of our fixed, intensively surveyed study area along the 314 m section of this stream is approximately 7437 m$^2$ (100 % minimum convex polygon of all captures). The nearest stream to which the neighbouring population is tied is about 500 m (Euclidean distance), and the salamanders also reproduce in other small streams flowing into the Vltava on both sides. The Vltava canyon here, north of Prague, forms a corridor in a highly urbanised landscape, and the abundance of small watercourses (first-order

**Table 1.** Capture effort and data collected.

| | 2017-18 | 2018-19 | 2019-20 | 2020-21 | 2021-22 | 2022-23 | 2023-24 | 2024-25 |
|---|---|---|---|---|---|---|---|---|
| capture events | 22 | 43 | 42 | 27 | 24 | 36 | 30 | 35 |
| adult males | 44 | 153 | 167 | 245 | 183 | 283 | 371 | 362 |
| adult females | 34 | 92 | 143 | 112 | 136 | 179 | 191 | 202 |
| non-adults | 10 | 36 | 29 | 19 | 15 | 51 | 111 | 123 |
| unique adult males | 32 | 61 | 73 | 108 | 99 | 113 | 139 | 132 |
| unique adult females | 25 | 45 | 71 | 72 | 76 | 86 | 94 | 93 |
| unique non-adults | 8 | 24 | 22 | 15 | 11 | 34 | 69 | 77 |
| unique adult (more than one-capture) males | 25 | 55 | 71 | 99 | 95 | 109 | 128 | 107 |
| unique adult (more than one-capture) females | 18 | 39 | 58 | 66 | 67 | 73 | 85 | 70 |
| unique non-adult (more than one-capture) | 2 | 8 | 10 | 8 | 6 | 21 | 42 | 37 |
| first-capture males | 32 | 35 | 38 | 35 | 14 | 14 | 24 | 18 |
| first-capture females | 25 | 32 | 36 | 21 | 17 | 25 | 23 | 23 |
| first-capture non-adults | 8 | 22 | 18 | 8 | 8 | 23 | 55 | 55 |

streams, mostly without fish) in shady canyons provides the salamanders with a suitable aquatic environment for larval deposition and development. It is questionable to what extent this dispersal through the river valley is due to migration of individuals after metamorphosis, and to what extent larvae washed into the river from streams are able to survive in the unfavourable river conditions. The population we studied cannot be considered isolated and we expected it to be an open population. Other amphibian species living in the same area include *Bufo bufo*, *Rana temporaria* and *R. dalmatina*.

## Sampling method

The period of surface activity is divided into two parts, separated by a summer (approx. half of June – half of August) and a winter (approx. end of November - end of February) pause (Catenazzi 1998; Schmidt et al. 2014). This separation is not completely 100%, but the activity of the salamanders on the surface is strongly dampened during these intermediate periods. The winter records in particular are exceptional. As we started visiting the area in July 2017, each of our annual periods, to which the following calculations refer, starts on 1 July and ends on 30 June of the following year. When weather conditions (rain and temperature) were suitable, we also visited the study area during periods of inactivity. However, the data on capture event counts in Table 1 are only relative to days with salamander records.

As fire salamanders are mainly active at night and only when humidity is high (Schulte et al. 2007), most of the captures were made during rainy nights, but not exclusively. If it started to rain during the day, the area was also searched for salamanders during the day. Salamanders were always searched for in a fixed area by visual encounter surveys by a single (always the same) observer. As the accuracy of GPS is low in dense forest canopy, we identified the positions of prominent trees and other landmarks in advance and measured the position of each salamander from these field marks. Salamanders were photographed from above, from below (cloacal part) and the right parothoid gland was also photographed. Only juvenile and subadult salamanders were measured to the nearest 5 mm. Salamanders larger than 140 mm were considered adults (Najbar et al. 2020; Seifert 1991; Speybroeck and Steenhoudt 2017). Some authors report even smaller sizes (e.g., Alvarez et al. 2015; 110 mm). All salamanders were released immediately at the place of capture without any marking. A negative behavioral response to capture as a result of handling techniques (Bailey et al. 2004; Price et al. 2011), influencing the probability of recapture (trap-shy effect), was very unlikely due to the low level of stress. Our study population belongs to the subspecies *S. s. salamandra*, which is characterised by a black background with contrasting yellow spots. The number and shape of these spots are highly individually variable, and the dorsal pattern of adult fire salamanders has traditionally been considered stable over time (e.g. Carafa and Biondi 2004; Feldman 1967; Klewen 1991). Balogova et al. (2016) and Beukema (2011) mention the ontogenetic development of the dorsal pattern, the increase in the number of spots changing from a more rounded to an irregular shape, and the splitting of coherent larger spots into smaller ones. However, these changes are of minor importance in sexually mature adults and do not hinder individual identification (Bogaerts 2002; Speybroeck and Steenhoudt 2017). Ontogenetic development of yellow spots also occurs in our salamander population, but the colour pattern was stable enough to allow identification of adult salamanders that measured 70 mm when first captured as juveniles. The smallest post-metamorphic fire salamanders are reported to measure 40-60 mm (Najbar et al. 2020; Kiss et al. 2021; Seifert 1991). Sex was determined by visual inspection of the cloaca (males have a swollen cloaca, especially during the breeding season) and body proportions (males have slenderer bodies, longer tails and longer limbs) (Labus et al. 2013; Rebelo and Leclair 2003).

We have tried to use the automated image analysis tools for salamander identification such as I3S (Van Tienhoven et al. 2007), WildID (Bolger et al. 2012), AmphIdent (Drechsler et al. 2015) and APHIS (Moya et al. 2015), but these tools are sensitive to the correct positioning and illumination of the highly ‚3D‘ salamanders (Schulte et al. 2024), otherwise the error rate is high. We can agree with Speyenbroeck and Steenhoud (2017) that it is not easy to correctly position live salamanders, and it is quite difficult to keep them still while photographing them under non-easy field conditions (night, rain, dense shrubs, insects attracted by the flashlight, steep muddy slopes and moving salamanders all around). Despite the considerable time involved, direct comparison of the photos with the gradually built up photo database of individuals proved to be the most effective and we used it.

Capture effort and data set are summarised in Table 1. The total capture effort was 259 events, with 22-42 capture events per year. In addition to 394 juvenile and subadult salamanders (212 unique individuals), we captured 1808 adult males and 1089 adult females, corresponding to 281 unique adult males and 235 unique adult females.

## Statistical analyses

The Cormack-Jolly-Seber (CJS) models (Lebreton et al. 1992) are mark-recapture models used to estimate two parameters: survival ($\Phi_t$, the probability of an animal surviving and remaining in the study area between time $t$ and $t+1$) and recapture probability ($p_t$, the probability of encountering a live animal at time $t$) (Williams et al. 2002). The four basic assumptions of these models are: (1) each marked salamander present in the population at time $t$ has the same probability of being recaptured ($p_t$) (equal detection assumption), (2) each marked salamander in the population immediately after time $t$ has the same probability of surviving to time $t+1$ (equal survival assumption), (3) marks are not lost or missed, and (4) marked salamanders are released immediately after sampling, and sampling is essentially instantaneous compared to the interval capture between events $t$ and $t+1$.

The estimated survival probability of transient and resident salamanders combined is the product of the net survival probability and the study area fidelity, i.e. the complement of transiency (Dzul et al. 2023; Schaub and Royle 2013), so we use the term ‚apparent survival‘ here. Because the study area fidelity of our residents is equal to one, we refer to it as ‚net survival‘. Where we do not distinguish between transients and residents, we use the term ‚survival‘.

CJS models are useful tools for testing hypotheses about what drives differences in survival and recapture probability. However, it is important to assess the goodness of fit (GoF) of these models before making inferences. The GoF of our full-parameter CJS model was used to test assumptions (1) and (2) using library (R2ucare) (Gimenez et al. 2018). Contrasting and individually specific colour patterns were used to identify individuals to satisfy assumption (3). Multiple captures of an adult individual in the same year were counted as a single capture, and captures in subsequent years were defined as a recapture to ensure assumption (4). This approach also eliminates the trap heterogeneity, which is reduced when many capture events within a season are combined into a single event (Angelini et al. 2010). When assessing the fit of the CJS models (assumptions (1) and (2)), we found a lack of fit of the ‘Test 3’, namely its component ‘Test 3SR’ for both males ($P = 0.016$) and females ($P < 0.001$). The other tests were not significant. As it is unlikely that photo-identification could affect salamander mortality, and the trap dependence/avoidance (Willson et al. 2011) is not relevant due to the methodology used, we considered the result of these tests to be a consequence of the presence of transients in the population (Genovart and Pradel 2019; Madon et al. 2013; Schmidt et al. 2005).

We used library(RMark) (Laake et al. 2022) to fit two age-class models of survival probability/transience, where age in a mark-recapture context is the time elapsed since first capture. It means that we split the salamanders (separately males and females) into two groups: (a) seen from >0x to =1x (e.i., only one year), (b) seen from >1x to =8x (e.i., more than one year). Transients were therefore included in the first age-class, whose survival is the product of the survival of the second age-class by the proportion of residents among the unmarked (Gimenez et al. 2017; Madon et al. 2013; White and Cooch 2017). The two age-class model with probability of survival/trancience fit the data well, and the lack of fit was not significant for males ($P > 0.05$) or females ($P > 0.05$). Our models were based on live captures only, and we tested the time effect on the survival and recapture probabilities in the open population for each annual period, maintaining the two age structure on survival. We developed four models based on the assumption that survival and recapture probabilities were constant or time-dependent. As we found some evidence of overdispersion, the variance inflation factor ($c$^) was calculated using library(R2ucare) (Gimenez et al. 2018) and used to calculate QAICc values (Burnham and Anderson 2002), which account for overdispersion (Mazerolle 2006). Consequently, we estimated the size of the resident population, the annual survival probability, the life span of adult residents as $1/-\ln(\Phi)$ (Angelini et al. 2010; Seber 1982), and the proportion of transient individuals in the population. We considered individuals that we encountered only once and then left the study area to be transient (Angelini et al. 2010; Pradel et al. 1997) and considered them as evidence of migratory activity (Schmidt et al. 2007).

Site fidelity vs. transiency/dispersal was also tested by considering the distance between the first capture point for each salamander and the points where it was

**Table 2.** Model selection statistics for supported CJS models. Φ(age) = survival constant (two-age class structure), Φ(age*time) = survival time-dependent (two-age class structure), p(.) = recapture constant, p(time) = recapture time-dependent. Given are: AICc = Akaike information criterion adjusted for small sample size; ΔAICc = AICc − minAICc; weight = relative likelihood of model, neg2lnl = likelihood ratios, chat = variance inflation factor (c^), QAICc = quasi-likelihood Akaike information criterion adjusted for small sample size.

| model | npar | AICc | ΔAICc | weight | neg2lnl | chat | QAICc |
|---|---|---|---|---|---|---|---|
| **males** | | | | | | | |
| Φ(age)p(.) | 8 | 1252.1 | 11.5 | 3.2e-03 | 1236.1 | 2.14 | 592.4 |
| Φ(age)p(time) | 14 | 1240.6 | 0.0 | 9.9e-01 | 1212.6 | 2.14 | 593.4 |
| Φ(age * time)p(.) | 35 | 1288.1 | 47.5 | 4.8e-11 | 1218.1 | 2.14 | 638.0 |
| Φ(age * time)p(time) | 41 | 1280.1 | 39.5 | 2.6e-09 | 1198.1 | 2.14 | 640.7 |
| **females** | | | | | | | |
| Φ(age)p(.) | 8 | 995.7 | 0.0 | 9.1e-01 | 979.6 | 1.9 | 529.2 |
| Φ(age)p(time) | 14 | 1000.3 | 4.7 | 8.8e-02 | 972.3 | 1.9 | 537.3 |
| Φ(age * time)p(.) | 35 | 1020.6 | 24.9 | 3.5e-06 | 950.6 | 1.9 | 567.9 |
| Φ(age * time)p(time) | 41 | 1029.7 | 34.1 | 3.7e-08 | 947.7 | 1.9 | 578.4 |

**Table 3.** Survival and recapture probability of the adult salamanders.

| | estimate | se | lower 95% Cl | upper 95% Cl |
|---|---|---|---|---|
| **males ‘Φ(age)p(.)’** | | | | |
| apparent survival probability (Φ) of residents and transients together | 0.80 | 0.03 | 0.74 | 0.85 |
| net survival probability (Φ) residents only | 0.91 | 0.02 | 0.88 | 0.94 |
| recapture probability (p) residents only | 0.74 | 0.02 | 0.71 | 0.78 |
| **females ‘Φ(age)p(.)’** | | | | |
| apparent survival probability (Φ) of residents and transients together | 0.70 | 0.04 | 0.63 | 0.77 |
| net survival probability (Φ) residents only | 0.90 | 0.02 | 0.86 | 0.93 |
| recapture probability (p) residents only | 0.69 | 0.02 | 0.64 | 0.74 |

recaptured. This distance is expected to be stable over time for sedentary individuals and tends to increase over time for transient/dispersing individuals (Bonato and Fracasso 2003). Since the time intervals between capture events were not normally distributed based on Shapiro-Wilk tests, we used Wilcoxon rank-sum tests to determine if there were significant differences between sexes in the compared metrics.

To address the question of where the transients occurred in the resident area, we used the R function ‘adehabitatHR::kerneloverlap(method=‘HR’)” (Calenge and Fortmann-Roe 2015) and calculated kernel density estimation (KDE) of all captures of single-capture salamanders and KDE of all captures of multi-capture salamanders and then we calculated their overlap. The smoothing factor has been scaled so as to generate an area equal to that recorded at 100 % MCP (Downs and Horner 2008; Row and Blouin-Demers 2006). To asess possible spatial inhomogeneity of transience probability more thoroughly, we expanded the constant transience model fitted and discussed before by adding a covariate describing the distance along the stream (flowing in the center of our research area) from a reference point downstream. To this end, we took for each animal centroid of all of its capture positions based on the function sf::st_centroid() (R Core Team 2023), projected it onto the stream curve and measured the distance from the projection to the reference point and took both linear and quadratic trends as covariates in the CJS model survivals. This allowed us to estimate the dependence of the transience probability on the distance along the stream and hence check its spatial homogeneity in a much more specific (and hence also more sensitive) way compared to the kernel density approach. We fitted the along-stream-heterogeneous-transiency model (ASHM) separately for males and females.

We hypothesised that transients were attracted to the study area by the presence of the breeding stream. As our study area is highly 3D structured, we compared Euclidean distances (stats::dist(method = euclidean)) of single and multi-capture adult salamanders from the stream. In addition, we explored the effect of the position along the stream on the probability of transience in a formalized way – in a CJS model with covariate.

## Results

### Survival, recapture and lifespan estimation

The model with the best fit on the basis of QAICc after applying the variance inflation factor (*c^*) was a two-age class model with constant survival and constant recapture probabilities ‘Φ(age)p(.)’ for both males and females (Table 2).

The mean annual apparent survival probability of adult residents and transients together was 0.80 (95%

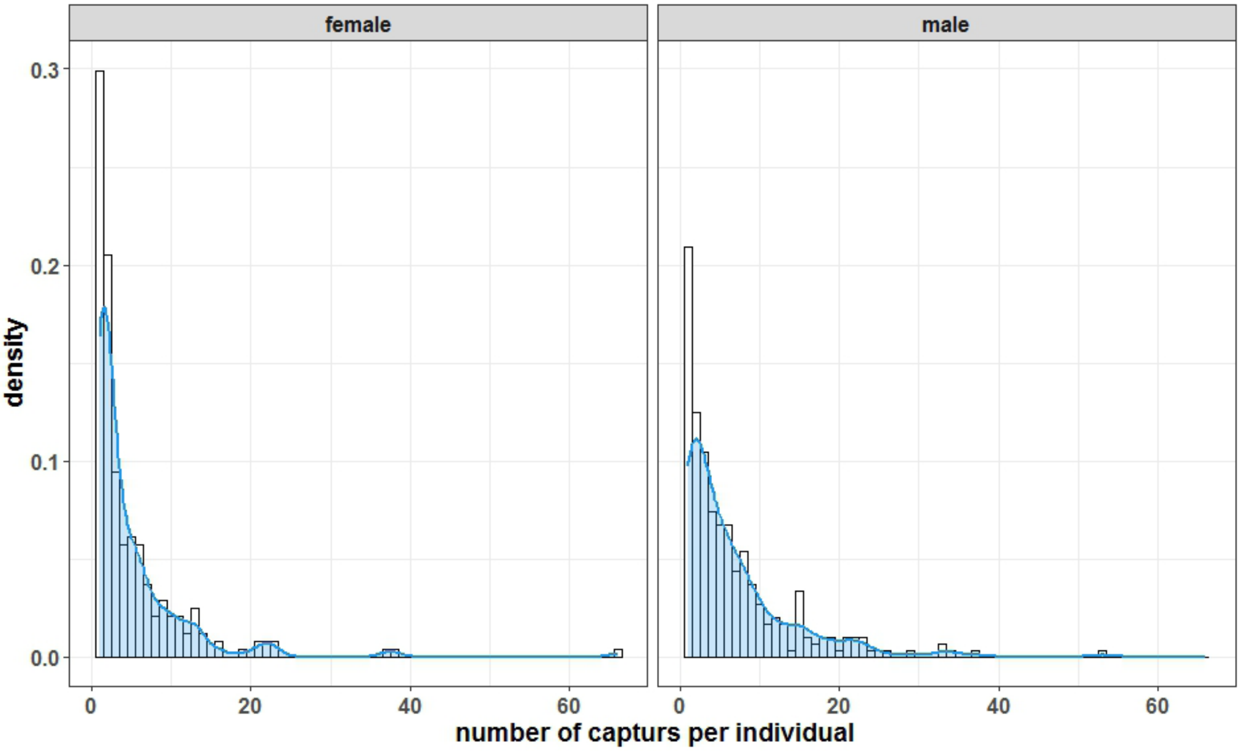

**Fig. 1.** Density histogram showing the distribution of capture numbers per adult individual.

CI = 0.74 - 0.85) for males and 0.70 (95% CI = 0.63 - 0.77) for females, respectively. The mean annual net survival probability of adult resident males and females was 0.91 (95% CI = 0.88 - 0.94) and 0.90 (95% CI = 0.86 - 0.93), respectively. The mean annual recapture probability of adult resident males and females was 0.74 (95% CI = 0.71 - 0.78) and 0.69 (95% CI = 0.64 - 0.74), respectively. The mean estimated life span after sexual maturity i.e., resident adult life expectancy, was 10.6 yr (95% CI = 7.5 – 15.1) for males and 9.7 yr (95% CI = 6.5 – 14.6) for females (Table 3).

## Population size and abundance trends

The number of unique adult males and females seen ranged from 32 to 139 and 25 to 94, respectively, depending on the year. The number of unique resident (more than one capture) adult males and females seen ranged from 25 to 128 and from 18 to 85, respectively, based on year. The number of first-capture adult males and females ranged from 14 to 38 and 17 to 36, respectively, depending on the year (Table 1). Because we estimate recapture probabilities, we cannot estimate abundance in the first year. Population size estimates based on the best-ranked model, 'Φ(age)p(.)' ranged from 83.4 (95% CI = 72.0 – 102,9) to 205.4 (95% CI = 177.4 – 223.5) for resident adult males and from 63.9 (95% CI = 54.2 – 75.5) to 146.0 (95% CI = 133.6 – 160.8) for resident adult females (Table 4, Figure 2).

The distribution of recaptures per adult individual is shown in Figure 1. There was a significant (W = 28306, *P* < 0.0001, Mann Whitney U Test) difference between the sexes in the mean number of recaptures (males: mean ± SD = 6.7 ± 7.1, max = 53, females: mean ± SD = 5.0 ± 6.7, max = 66).

The percentage of recaptures (i.e. animals captured at least twice) of adult salamanders within the capture event increased steeply to about 400 captured males and females, respectively. We reached these numbers in the third and fourth years of our capture activity, with 121 and 150 capture events for males and females,

**Table 4:** Estimated abundance of resident salamanders (means ± 95% CIs); fited model with two-age classes on survival and constant recapture 'Φ(age)p(.)".

| 0.0556 | | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| | | 2018-19 | 2019-20 | 2020-21 | 2021-22 | 2022-23 | 2023-24 | 2024-25 |
| males | lower 95% Cl | 72.0 | 86.0 | 133.3 | 117.7 | 138.0 | 177.4 | 151.6 |
| | mean | 83.4 | 102.1 | 145.8 | 138.0 | 160.2 | 205.9 | 173.8 |
| | upper 95% Cl | 102.9 | 124.9 | 166.8 | 151.3 | 177.1 | 223.5 | 186.7 |
| females | lower 95% Cl | 54.2 | 85.6 | 95.8 | 99.3 | 115.9 | 133.6 | 119.6 |
| | mean | 63.9 | 102.6 | 108.9 | 110.6 | 129.6 | 146.0 | 133.6 |
| | upper 95% Cl | 75.5. | 122.4 | 126.3 | 121.7 | 150.0 | 160.8 | 146.9 |

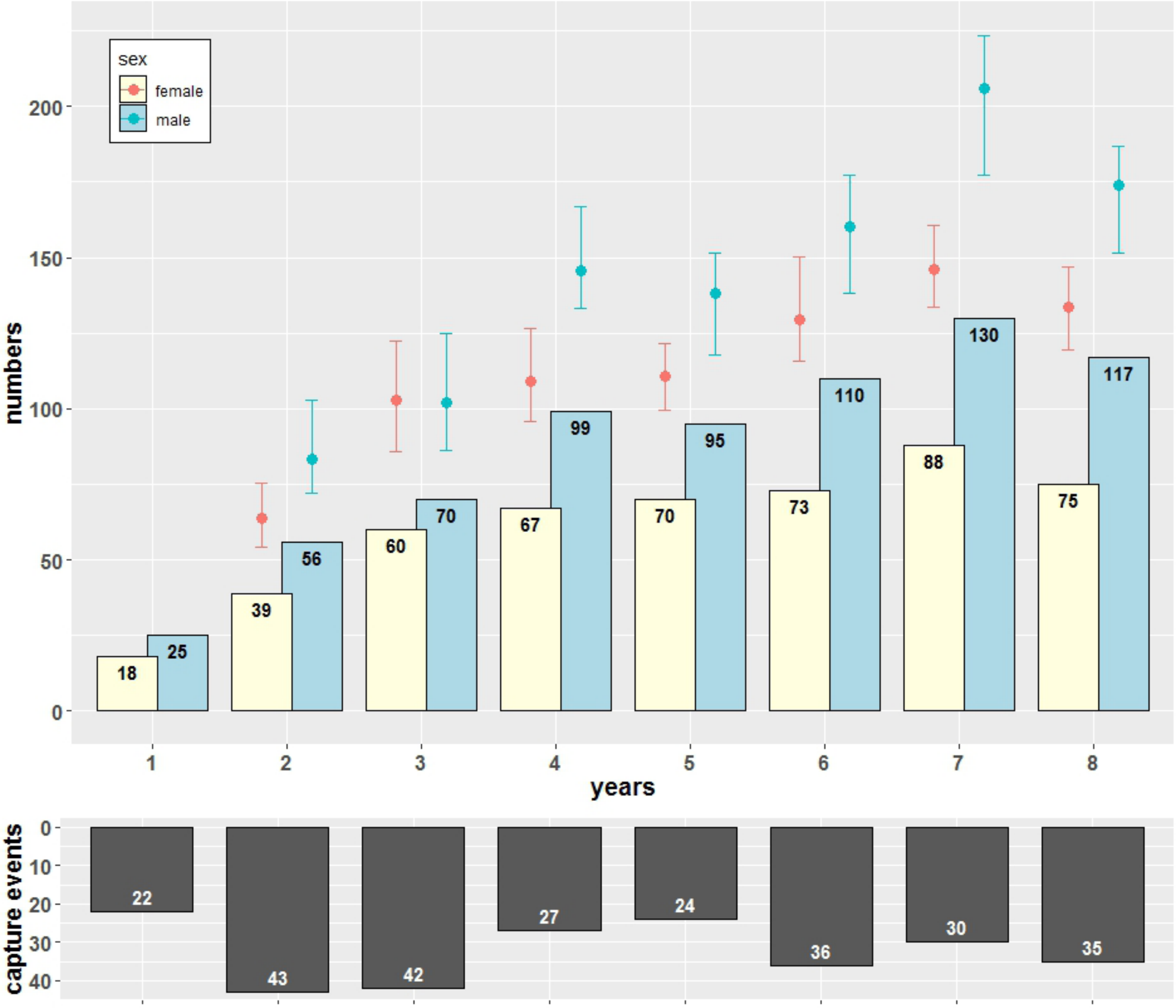

**Fig. 2.** Estimated year abundance of resident adult salamanders (means ± 95% CIs) (dots) based a two-age class model of survival and constant recapture ‘Φ(age)p(.)’ and the number of unique resident (more than one-capture) adult salamanders seen per year (bars). Each annual period starts on 1 July and ends on 30 June of the following year. The number of capture events in a given year is shown in the bottom part of the figure.

respectively.There was a break in the trend in this year and the mean estimate of the proportion of multi-captured adult salamanders in the searched population “stabilised“ in the range of 0.88 - 0.96 (95% CI of max value = 0.79 - 1.00) for males and 0.87 - 0.95 (95% CI of max value = 0.81 - 1.00) for females (Figure 3).

## Degree of transience, site fidelity vs. tendency to disperse

The phenomenon of transience revealed by the goodness-of-fit tests in the salamander population also appears to be non-negligible for males and females. The mean level of transience calculated from the model ‘Φ(age)p(.)’ was 0.13 (95% CI = 0.04 - 0.16) for males and 0.19 (95% CI = 0.09 - 0.28) for females.

The correlation between the distance between the first capture point and any other capture point for each salamander and the time elapsed was significant ($P < 0.05$) only for 31 males and 11 females, respectively, and not significant ($P > 0.05$) for 141 males and 104 females, respectively. Therefore, 18% of males and 10% of females showed tendencies towards a transiency / disperse (lack of range-resident behavior) and 82% of males and 90% of females showed tendencies towards a sedentary life. For both sexes, there was a significant negative relationship between the strength of this correlation and the total time between the first and last capture of a given adult individual (males: $R = -0.35$, $P < 0.001$, $n = 172$, females: $R = -0.289$, $P = 0.004$, $n = 115$) and also between the number of recaptures (males: $R = -0.35$, $P < 0.001$, $n = 172$, females: $R = -0.32$, $P < 0.001$, $n = 115$).

In addition to individuals that were recaptured repeatedly (Figure 1), the population also included individuals that were recaptured after a very long time (Table 5). The correlation of distance and time between these consecutive captures separated by long periods of time (2 or more years) was not significant for males ($P > 0.05$, $n = 45$, Pearson) or females ($P > 0.05$, $n = 38$, Pearson). There were many individuals of both sexes in

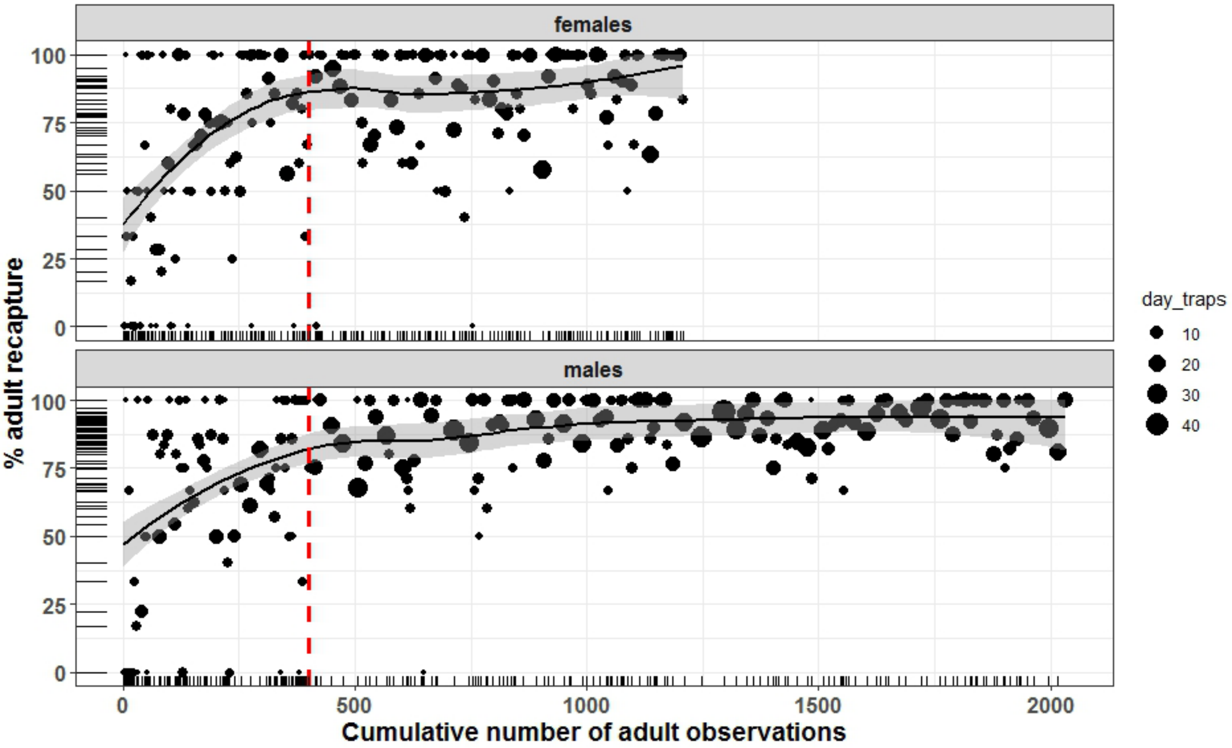

**Fig. 3.** Recapture rate of adult salamanders by capture event with non-parametric, locally weighted regression smoother (loess) and 95% CIs. The size of the points corresponds to the number of captures within the given capture event. A one-dimensional density plot is plotted on both axes of a graph in the form of a marginal rug. It can be used to observe the marginal distributions more clearly. The red dashed line represents a 400 adult observations, which corresponds to the beginning of the fourth year of the capture effort. The subsequent stagnation of the recapture rate suggests that the population is well trapped, meaning that the population estimates from our models can be considered reliable from this point onwards.

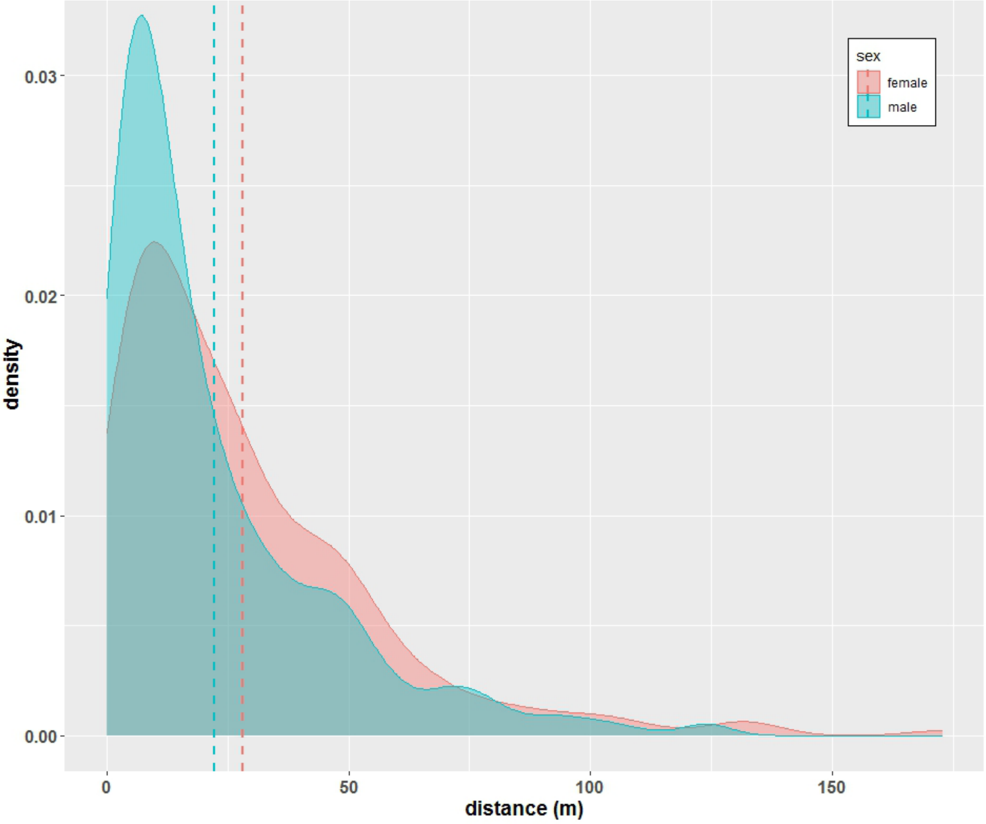

**Fig. 4.** Density histogram of annual distances between first and last capture of individuals with mean values (dashed line). Only individuals with 2 or more captures. The vast majority of adult salamanders lead sedentary lives, moving less than 50 m in a year - usually much less - reflecting stable population conditions.

**Table 5.** Time intervals between consecutive recaptures grouped by year.

| time interval | males | females |
|---|---|---|
| ≤ 1 year | 90.6% (*n* = 1336) | 84.2% (*n* = 691) |
| >1 years ≤ 2 | 7.5% (*n* = 110) | 12.1% (*n* = 99) |
| >2 years ≤ 3 | 1,5% (*n* = 22) | 2.7% (*n* = 22) |
| >3 years ≤ 4 | 0.4% (*n* = 6) | 1.0% (*n* = 8) |
| > 4 years | 0.1% (*n* = 1) | 0.1% (*n* = 1) |

**Table 6.** Distances between salamander captures during the year (annual period: from 1 July to 30 June of the following year).

| sex | year | The distances between the first and the last captures of individual | The distances between the furthermost captures of individual |
|---|---|---|---|
| | | mean ± SD, max, n | |
| males | 1 | 14±17, max=50, n=11 | 15±17, max=50, n=11 |
| | 2 | 24±24, max=103, n=39 | 29±26, max=103, n=39 |
| | 3 | 17±17, max=78, n=50 | 20±20, max=86, n=50 |
| | 4 | 20±21, max=97, n=67 | 25±24, max=97, n=67 |
| | 5 | 26±28, max=112, n=47 | 31±29, max=119, n=47 |
| | 6 | 22±23, max=126, n=81 | 32±26, max=136, n=81 |
| | 7 | 26±27, max=123, n=111 | 35±31, max=127, n=111 |
| | 8 | 20±19, max=111, n=81 | 33±25, max=112, n=81 |
| females | 1 | 9±7, max=23, n=7 | 12±12, max=39, n=7 |
| | 2 | 18±14, max=50, n=19 | 20±13, max=50, n=19 |
| | 3 | 18±21, max=90, n=33 | 25±22, max=90, n=33 |
| | 4 | 30±30, max=128, n=29 | 31±29, max=128, n=29 |
| | 5 | 29±25, max=112, n=31 | 37±29, max=112, n=31 |
| | 6 | 32±30, max=133, n=39 | 43±398, max=204, n=39 |
| | 7 | 31±26, max=133, n=54 | 40±29, max=133, n=54 |
| | 8 | 31±31, max=173, n=46 | 43±37, max=178, n=46 |

the population who remained in the same, or almost the same place, or returned to exactly the same place, even after 3 and even 4 years.

The distances between the most distant captures of individuals were (mean ± SD) 49 m ± 34 m (max = 160 m) for males and 58 m ± 43 m (max = 204 m) for females (Table 6). Differences between sexes were not significant ($W$ = 20094, $P > 0.05$, Mann Whitney U Test). The distances between the first and last capture of an individual were (mean ± SD) 25 m ± 26 m (max = 160 m) for males and 33 m ± 312 m (max = 177 m) for females (Table 6). Differences between sexes were significant ($W$ = 21181, $P < 0.01$, Mann Whitney U Test). The time intervals between the first and last capture of an individual with two or more caprures were (mean ± SD) 1088 days ± 786 days (max = 2773 days) for males and 1090 days ± 787 days (max = 2837 days) for females. Differences between sexes were not significant ($W$ = 18223, $P > 0.05$, Mann Whitney U Test). 89% of the males and 85% of the females moved less than 50 m in one year, 82% the of males and 74% of the females moved less than 40 m, 61% of the males and 50% of the females moved less than 20 m and 52% the of males and 41% the of females moved less than 15 m, respectively (Figure 4).

The distances between the most distant captures of individuals were significantly greater than the distances between the first and last captures for both sexes (males: $X^2$ = 32557, $P < 0.001$, Pearson; females: $X^2$ = 20947, $P < 0.001$, Pearson).

There was a significant ($W$ = 684656, $P < 0.0001$, Mann Whitney U Test) between-sex difference in the time intervals between consecutive recaptures for males (mean ± SD) 146 days ± 196 days (max = 1632 days = 4.47 yr) and females (mean ± SD) 191 days ± 237 days (max = 1745 days = 4.78 yr).

96% and 84% of the positions of single-capture males and females, respectively, lie within 95% of the KDE of all multi-capture individuals activities (Figure 5 left). The proportion of the kernel density estimation (KDE) area of all captures of single-capture salamanders covered by the KDE of multi-capture salamanders was 100% for both sexes. Estimates of the transiency changes along the stream are visible on the Figure 5 (right). It is clear from the figures that the transiency is far from being constant. It is the lowest in the middle part of the stream line going through our research area and higher at the lower and upper ends. In fact, transient probability is much higher for lower parts of the investigated stream than for the upper part. Both females and males show generally similar shape of the along stream transient dependency but the values are generally higher for females than for males, as expected.

The Euclidean distances of the salamanders from

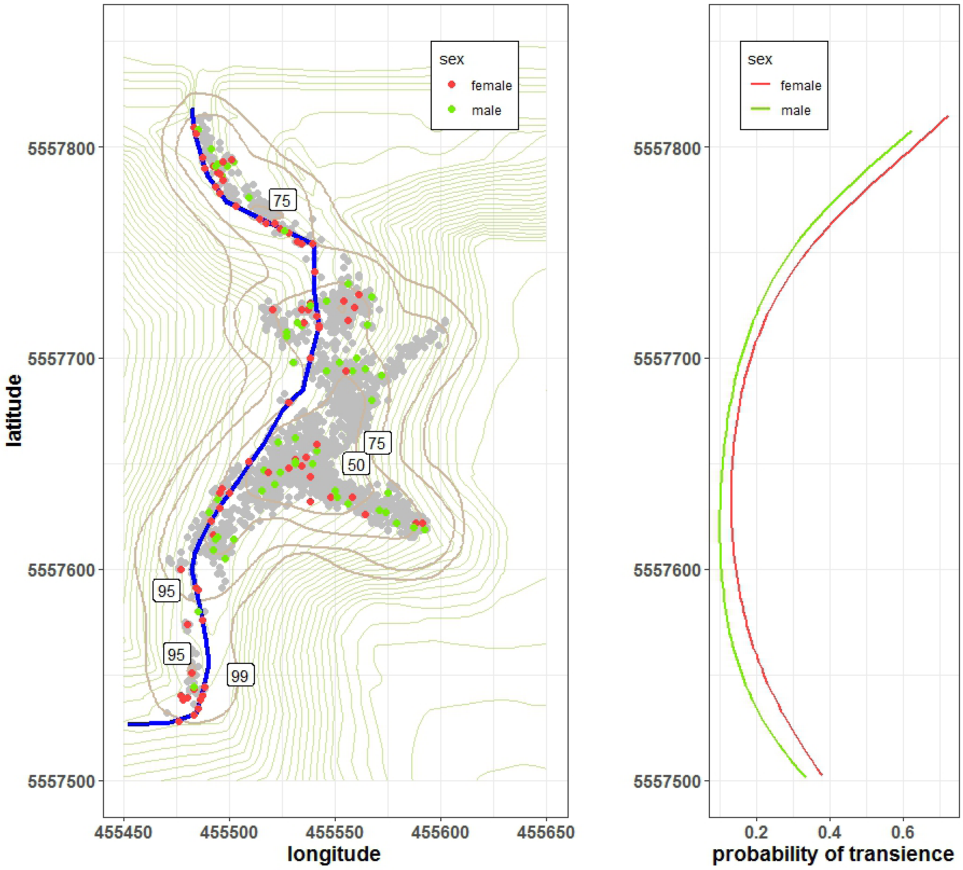

**Fig. 5.** The places with different levels of transience/residency in the study population. Left - location of single-capture adult salamanders (red and green dots) within the 99%, 95%, 75% and 50% kernel density estimation (KDE) area of all multi-capture adult salamander captures (gray dots). Blue line = reproduction stream flowing north, green curves = contour lines; Right – the transiency probability (0.0–1.0) changes along the stream, being lowest in the middle part (the core area of the population) and higher at the lower and upper ends.

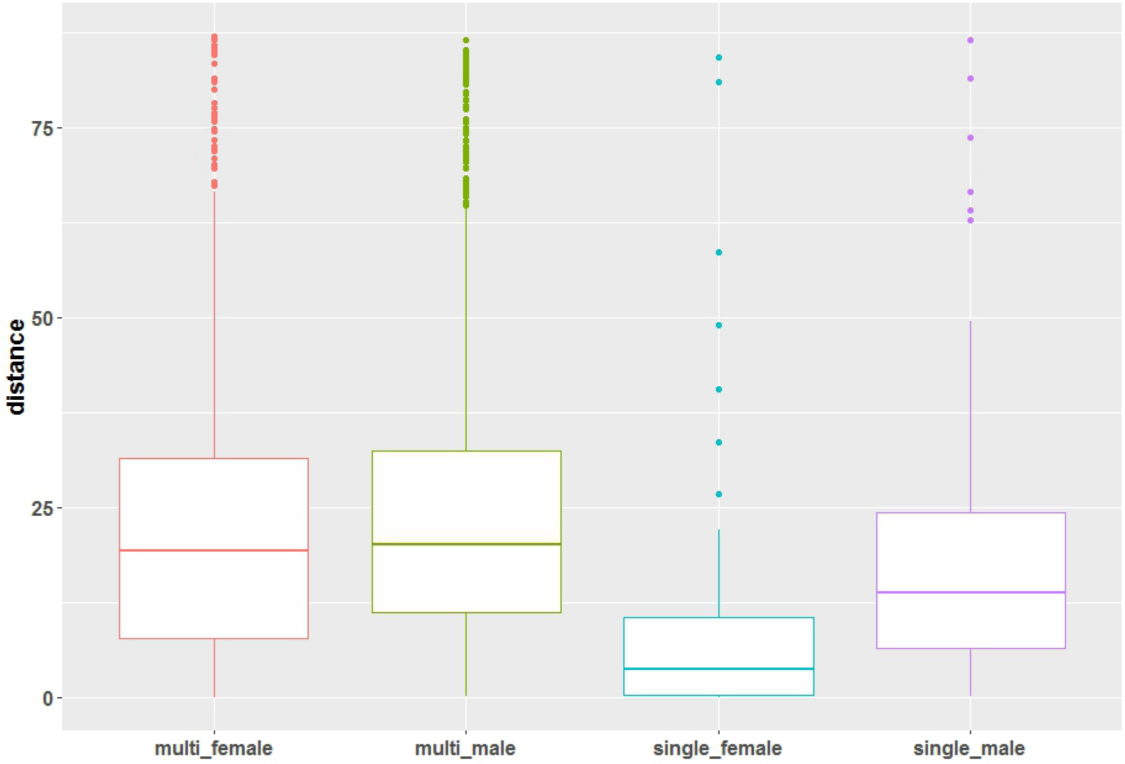

**Fig. 6.** The comparison of the Euclidean distances of transient and resident salamanders from the stream (single: 1 capture individuals, multi: >1 captures individuals), (median, 75th and 25th percentiles, largest values within 1.5 times the interquartile range above the 75th percentile).

the stream were as follows (mean ± SD): single-capture females 9.2 m ± 14.9 m (max = 86.2 m, *n* = 75), multi-capture females 23.8 m ± 19.1 m (max = 92.2 m, *n* = 1087), single-capture males 21.1 m ± 23.1 m (max = 91.5 m, *n* = 52), multi-capture males 26.5 m ± 20.1 m (max = 90.4 m, *n* = 1882). Single-capture females were located significantly closer to the stream than the multi-capture females (*W* = 63803, *P* < 0.001, Mann Whitney U Test), significantly closer than the single-capture males (*W* = 2898, *P* < 0.001, Mann Whitney U Test), and significantly closer than the multi-capture males (*W* = 177648, *P* < 0.001, Mann Whitney U Test), as well. This means that the transient females were found closer to the stream than resident salamanders of both sexes and than the transient males, as well (Figure 6).

The timing of the arrival of single-capture females, i.e. transient females, shows a clear peak in early spring: 11,6% (*n* = 17) of captures in March and 14,8% (*n* = 26) of captures in April), coinciding with the larval laying period. The timing of the arrival of single-capture males, i.e. transient males, does not show a seasonal peak (Figure 7).

## Discussion

### Lifespan, survival and recapture estimation

Survival of adult fire salamanders is a critical demographic metric of the population dynamics of these long-lived amphibians. Their terrestrial stages (i.e. variation in losses) are the most important determinants of population growth rate (Schmidt et al. 2005; Sinsch 2024), which contradicts the common assumption that amphibian population dynamics are driven by the larval stage (i.e. variation in recruitment) (e.g., Semlitsch 2003).

There is inter-population variation in the annual survival of the fire salamanders. Higher values of annual survival indicate a stable population and adult longevity, whereas lower values indicate a declining population due to higher emigration or mortality rates, or both. Depending on the locality and year, the annual survival probability of fire salamanders ranged broadly from 0.39 to 0.96 in Germany, Switzerland, Slovakia, Austria and Hungary (Balogova et al. 2017; Burgstaller et al. 2021; Cayuela et al. 2019; Kiss et al. 2021; Rebelo and Caetano 1995; Schmidt et al. 2005; Schmidt et al. 2007; Schmidt et al. 2014), regardless of sex (Kiss et al. 2021). The mean annual net survival probabilities of resident adults of both sexes from our locality (males: 0.91, females: 0.90) are in line with or even higher than estimates from the above studies, and our population could be considered stable. At the interspecific level, survival is also high for other true salamanders, e.g. 0.84 for *Salamandra infraimmaculata (*Altunisik 2018*),* 0.88 for *Salamandra lanzai* (Miaud et al. 2001), up to 0.79 for *Lyciasalamandra fazilae* and up to 0.90 for *Salamandrina perspicillata* populations (Cayuela et al. 2019), suggesting that long lifespan is a highly conserved trait in western Palaearctic salamanders (Cayuela et al. 2019). The long lifespan of salamanders is likely due to the combination of their high regenerative capacity (Cayuela et al. 2019), sedentary fossorial life (e.g., Alvarez et al. 2015; Joly 1968; Rebelo and Leclair 2003) and effective skin venom, which provides a strong antipredator and antimicrobial defence (Lüddecke et al. 2018; Sinsch 2024). Due to their fossorial lifestyle, neither winter nor summer are periods of increased mortality (Kiss et al. 2021; Schmidt et al. 2014). In comparison, mean annual survival estimates for plethodontid salamanders are

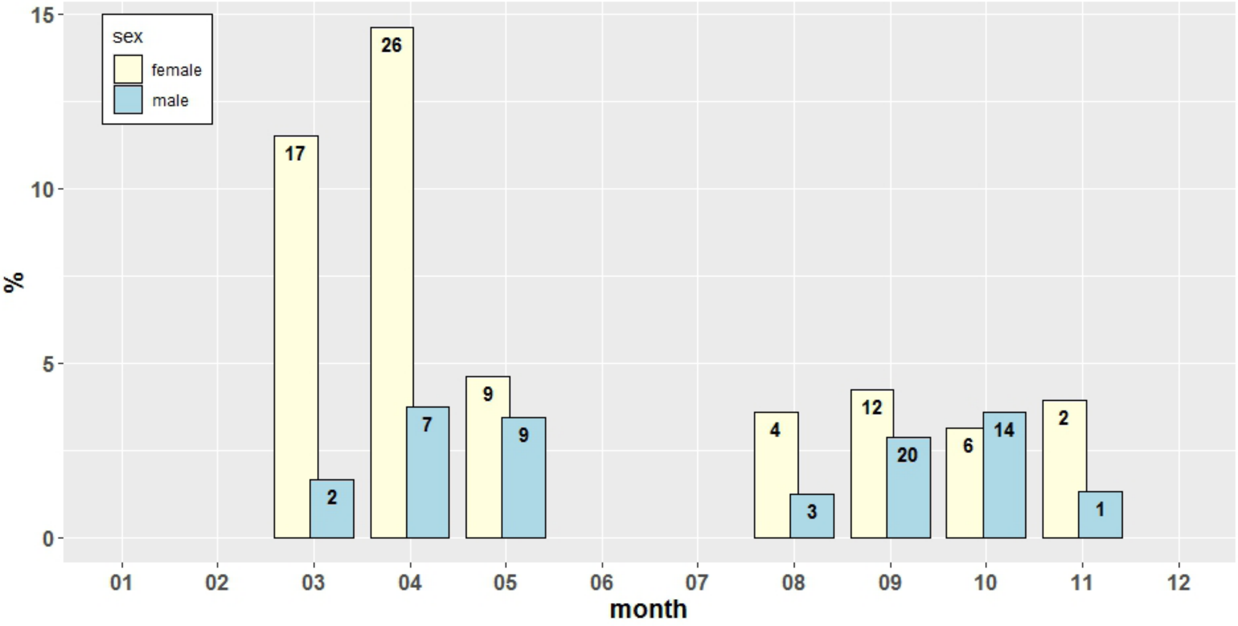

**Fig. 7.** Seasonal changes in the proportion of single-capture adult salamanders pooled by month, 8 yr together (numbers of single-capture adult salamanders are given in bars).

reported to be as low as 0.43 (Danstedt 1975) or even lower (Price et al. 2012) and for salamanders of genus Ambysoma 0.45 – 0.65 (Blackwell et al. 2004; De Lisle and Grayson 2011; Douglas and Monroe 1981; Homan et al. 2018; Williams 1973).

Balogova et al. (2017) and Burgstaller et al. (2021) report higher values of survival of males compared to females. However, this difference is likely only an artefact of higher aboveground activity of males and does not reflect higher emigration or mortality of the resident females (Burgstaller et al. 2021; Kiss et al. 2021). At our locality, the aboveground activity of males was also higher than that of females, but the net survival of resident males and females was very similar, and this is further supported by the fact that there were no sex differences in the mean time interval between the first and last capture of an individual over the course of our eight-year study.

The mean annual recapture probability of adult residents was quite high: 0.74 for males and 0.69 for females at our locality, which is not always very common for salamanders e.g., *Ambystoma maculatum* 0.16-0.67 (Homan et al. 2018), *Ambystoma maculatum* 0.36–0.73 (Blackwell et al. 2004), *Salamandra salamandra* 0.19-0.46 *(*Burgstaller et al. 2021), *Plethodon* spp. 0.19 (Bailey et al. 2004). Our figures indicate that if an individual adult salamander, regardless of sex, was alive, there was a high probability that it would be recaptured, regardless of the high level of underground life. This finding is important for subsequent estimates based on CJS models, as their accuracy can be low when either survival or detection probabilities are low (Wagner et al. 2011).

The lifespan of *S. salamandra* ranges from 7 to 33 yr, depending on the author, estimation method and location (e.g., Gäbler 1935; Joly 1968; Kalezic et al. 2000; Kiss et al. 2021; Najbar et al. 2020; Rebelo and Caetano 1995; Rebelo and Leclair 2003; Seifert 1991), and Böhme (1979) even mentions more than 50 yr in captivity. The 7-9 year age classes of *Salamandra salamandra* dominated (43.1%) in the Polish population (Najbar et al. 2020) and the 3-4 yr age classes dominated (44.5%) in the Hungarian population (Kiss et al. 2021). These differences probably reflect different recruitment of young age cohorts. The longevity of closely related species is reported to be 11-23 years for *S. infraimmaculata* (Altunisik 2018; Warburg 2007), 24 years for *S. lanzai* (Miaud et al. 2001), 20 years for *S. algira* (Reinhard et al. 2015) and 10-17 years for *S. atra* (Fachbach 1978; Kalezic et al. 2000). All these species are characterised by a slow life history strategy (i.e. low annual fecundity and high adult survival), and their mortality rate remained stable regardless of age (Cayuela et al. 2019). Salamanders of both sexes reach maturity at the age of 3-4 yr (Altunisik 2018; Kazelic et al. 2000; Kiss et al. 2021; Rebelo and Caetano 1995; Sinsch 2024; Warburg 2007), depending on the altitude and latitude (Flageole and Leclair 1992; Wilbur 1977), i.e. the climatic conditions of the area, so that overall life expectancy in our lowland population is approximately 14 yr (95% CI = 11 - 18) for resident males and 13 yr (95% CI = 10 - 18) for resident females. This estimate is in line with data published by other authors (e.g., Sinsch 2024).

## Population size and abundance trends

The ‘surface population’ and the ‘superpopulation’ of salamanders in a study area should be distinguished (Bailey et al. 2004; Wagner et al. 2011). Many fire salamanders are subterranean in a given moment, making them inaccessible for capture. Resident females leave their underground shelters less often than resident males (Homan et al. 2018; Kiss et al. 2021). The difference between the number of individuals seen on the surface and the population size estimated by the CJS models, corresponding to a ‚superpopulation‘, reflects this difference. In any given year, only 68 - 76% of resident males and 64 - 70% of resident females were observed compared to the mean estimated numbers. The greater difference in females reflects their lower willingness to come out of shelters.

The sharp initial increase in the proportion of recaptured salamanders began to slow down rapidly after 121 and 150 capture events for males and females, or after approximately 400 salamanders of both sexes were seen (Figure 3). Despite the differences in population sizes, it can be noted that the curves expressing this trend and the final proportion of recaptured versus first-captured salamanders are similar to the results of Speybroeck and Steenhoudt (2017), and both reflect population trends without fluctuations. It can therefore be assumed that the first-captured adult salamanders were already individuals newly arrived from the surrounding areas, i.e. true transients, in the fourth year of the capture effort. There were still many individuals in the population that we had not been able to capture before and that were new to our captures. Adults ‘hidden’ in the population as non-adults have also been identified, as our photo database of captures includes semi-adults and juveniles. Although some changes in spots still occur in these individuals, the changes are not significant (and are gradual) enough to prevent correct identification of the same individual. Therefore, estimates from our models can only be considered relevant from the fourth year of capture. Population size estimated in this period ranged from 146 (95% CI = 133 - 167) to 206 (95% CI = 177 - 224) for resident adult males and 109 (95% CI = 96 - 126) to 146 (95% CI = 134 - 161) for resident adult females. Until then, the initial increase in abundance (Figure 2) does not reflect real changes in the population, but is the result of under-capture of the population. Given that the effort to search for salamanders was approximately the same from year to year (see capture events in Table 1), this is probably a consequence of the hidden life of these highly fossorial amphibians (Rebelo and Leclair 2003).

## Degree of transience, site fidelity vs. tendency to disperse

Based on the tendency to disperse or live a sedentary life, Lowe et al. (2006) defined two individual strategies in a salamander population: ‘movers’ and ‘stayers’. The low proportion of movers indicates temporally stable conditions in the population (Dieckmann et al. 1999; McPeek and Holt 1992). Conversely, a high rate of dispersal, i.e. many transients in the population, suggests that either the spatial extent of salamander populations is underestimated or that migration rates between populations are high (Schmidt et al. 2007) due to temporally unstable habitat conditions (Travis 2001). The size of our search area, based on the two most distant captures, was 287 m and no individuals were detected crossing this distance. The two longest distances between the most distant captures of an individual were 204 m and 366 m (outside the regularly searched area), and the mean distance between the most distant captures was 49 m for males and 58 m for females. Thus, the spatial extent of our search area was probably not underestimated, but the closest stream to which the neighbouring salamander population is tied is about 500 m away from our stream, so exceptional successful migrations between these two populations cannot be ruled out.

We calculated the transinece level in two ways: from the CJS model and by comparing the distance between the first capture point for each salamander and the points where it was captured again. Both methods show a weak tendency to dispersal in our population: about 13% of transients for males and 19% of transients for females based on the CJS model. Long-term recaptured individuals showed a tendency towards a sedentary lifestyle, while short-term recaptured individuals showed a tendency towards dispersal. Older age classes were also more common among residents than among transients in the study by Rebelo and Leclair (2003). Burgstaller et al. (2021) found that most recaptured individuals moved less than 50 m within the same year, and our results are consistent (89% of the males and 85% of the females moved less than 50 m in one year, 52% the of males and 41% the of females moved less than 15 m in one year). The differences between the sexes were not significant. Our results confirm the presence of ‚movers‘ and ‚stayers‘ in the population (possibly a gradient in the tendency to disperse inside and/or outside the area). The majority of adult males and females lived a sedentary life, but a small proportion of individuals were transient. Low levels of dispersal/trancience reflect temporally stable conditions in our population.

The transient value could be overestimated by the phenomenon of temporary emigration. For the purpose of modelling population parameters, we distinguished two categories of ‚movers‘: ‚real transients‘, i.e. salamanders that left the study area without subsequently arriving, and ‚temporary emigrants‘, i.e. salamanders that left the study area for a while and then returned, or stayed underground for a long time. Temporary emigrants were assigned to residents.

We recaptured most of the salamanders in a single year, but the recapture history of several individuals included long gaps between consecutive captures. These gaps could be the result of either temporary emigration from the study area or long stays underground (Bailey et al. 2004; Petranka 1998; Price et al. 2012). The fact that the correlation of distance and time between these consecutive finds, separated by a long period (2 or more years), was not significant for either sex, and that some individuals were still found in identical locations after 3 to 4 years, suggests that these were individuals that had remained underground for a long time. The time intervals between consecutive recaptures were shorter for males, and the number of recaptures per individual was greater for males than for females, as in the study by Burgstaller et al. (2021) in Austria. This means that males appeared on the surface more often than females. Our value of transience was not affected by this temporary emigration (either real or underground), as the duration of our study was long enough to detect such an individual (Table 5).

However, the phenomenon of temporary emigration and precise homing does exist and salamanders are capable of long movements: 500 m (Burgstaller et al. 2021) or even 1900 m (Hendrix et al. 2017), sometimes in a short time (35–375 m per night: Rebelo and Leclair 2003; Schulte et al. 2007). The fastest movement we recorded was a female that moved 133 m in two days. However, there were not many such movements. Our results are consistent with the findings of Rebelo and Leclair (2003) that most individuals remain at the same site for many years, but several residents could be seen occasionally away from their usual site, then returning to it. We documented the movement of one resident female from her long-standing shelter in a tree stump to the stream at a distance of 25 m. She had laid larvaes there and then returned to exactly the same hole in the tree stump less than 14 days later. This female was recaptured 66 times over 8 yr in areas of 779 and 110 m$^2$ (95% and 50% KDE home range) and 321 m$^2$ (95% minimum convex polygon), respectively. Most of the time she did not move more than 5 m from her stump shelter. The occasional temporary emigration and subsequent homing behavior is also supported by the fact that the distances between the most distant captures of individuals were significantly greater than the distances between the first and last captures for both sexes in our population.

Transients did not occur at the edge of the resident area or in separate area(s), but the transience of both sexes changed along the stream, being lowest in the middle part of the stream line running through our area and higher at the lower and upper ends. This probably reflects the quality of the terrestrial habitats along the stream and indicates the location of the core area of the population studied. The generally higher transient probability of females than males, regardless of the part of the stream, is consistent with our other findings. The transient females were closer to the stream than resident salamanders of both sexes and than transient males. The transient behavior of females is therefore a consequence of their spring migration to the breeding stream likely, followed by their return to their own resident areas somewhere beyond the boundary of our study area. The timing of the appearance of single-captured females in the study area supports this explanation. In contrast, the appearance of single-captured males, concentrated mainly in the autumn period, reflects their increased mating activity or search for females.

## Conclusion

During our eight-year study, we examined the population dynamics of the fire salamander (*S. salamandra*) in a population that is not currently facing any serious anthropogenic threats. We focused on the following parameters: lifespan, survival, recapture estimate, population size and abundance trends, degree of transience and site fidelity vs. tendency to disperse.

Higher values of mean annual net survival of our salamanders compared to other European populations indicate a stable population and adult longevity. The total life expectancy of the resident salamanders in our lowland population is approximately 14 yr (95% CI = 11 - 18) for resident males and 13 yr (95% CI = 10 - 18) for resident females (resident adult life expectancy is minus 3 yr).

Low levels of dispersal/trancience reflect temporally stable conditions in our population. Most adult fire salamanders of both sexes live a sedentary life here, remaining for many years, perhaps most of their lives, in a small area close to their underground shelters. They leave these shelters infrequently and irregularly, mainly during the night rainfalls. Even during these climatically favourable events, most of the population remains underground, and the recapture history of several individuals includes long gaps between consecutive captures. The above ground activity of males is higher than that of females. This site tenacity can be a consequence of their hight level of independence from the aquatic habitats (Mathias et al. 1995). The absence of sex differences in site tenacity suggests that the availability of refuges with suitable microclimatic conditions as retreat sites with food resources around or inside them, rather than easy access to larviposition sites, is a dominant factor influencing the distribution of fire salamanders in the area (Rebelo and Leclair 2003). Fire salamanders spend most of their lives in these shelters, so the quality of these shelters is critical to the fitness of their owners. Drought, or climate more generally, is likely to be a primary driver of both local and spatially structured salamander population dynamics (Church et al. 2022), and the availability of suitable shelters could mediate mortality risks due to desiccation (Rothermel and Luhring 2005). High-quality shelters are not common, and contrary to the findings of Rebelo and Leclair (2003), shelters in our area were sometimes occupied by more than one salamander, but we agree that the crevices between tree root systems or stone walls are attractive retreats.

Most of our salamanders remain at the same site for many years, but some individuals were occasionally seen away from their usual sites (the longest relocation = 366 m, i.e. outside the regularly searched area), after which they return to it, and precise homing behavior exists. Our results confirm the presence of ‚movers‘ and ‚stayers‘ in the population, but the proportion of adult transients was low, indicating temporally stable conditions in the population. The level of transience was similar for both sexes. The transient behavior of females is triggered by the need to visit the breeding stream in spring. The transient behavior of males did not show any temporal or spatial pattern.

Knowledge of changes in abundance is essential for assessing the status of populations (not only) of fire salamanders. Estimates of demographic parameters based on direct counts are strongly underestimated for the fossorial salamanders compared to estimates based on capture-recapture modelling. CJS models can provide relevant results for open fire salamander populations. In demographic studies of cryptic animals based on the capture-recapture method, it must be taken into account that, in the initial period, estimates are biased by the lack of recapture of the population, as was the case here. Our initially lower population size estimates are mostly a consequence of lower initial numbers of captured individuals (since the estimates are essentially the number of captured individuals divided by the resight probability, which is constant in our model). Comparing our abundance estimates in the second and third years with the average abundance for the remaining stable period reveals an underestimation of approximately 49% and 37% for males and 48% and 17% for females, respectively. Since we estimated recapture probabilities, we could not estimate abundance in the first year. The lower number of individuals captured in the first three years probably reflects our limited knowledge of the study area, as well as the cryptic nature of salamanders. However, the estimates of the parameters ‚Φ‘ (i.e. the annual survival probability), longevity, and the proportion of transients in the population were unaffected by the under-capture of the population in the first three years. Therefore, the estimates can be considered relevant, indicating a stable population unaffected by significant stressors. For larger populations, especially those inhabiting difficult-to-search terrain, this underestimation will likely be greater, and it will take longer for the estimates to become relevant. Therefore, it is clear that several initial years that do not provide relevant results must be allowed for in order to assess the extent to which a given population is exposed to stress factors and changes in abundance. If ‚Φ‘ still deviates significantly from our findings after this period or if a decline in population size or an increase in the proportion of transients is detected, it is likely that the population is experiencing problems, such as long-term changes to water quality, degradation or fragmentation of the surrounding terrestrial habitats, conversion of the stream into a drainage channel that drains large paved areas, or threats from chytrid infection or the introduction of trout.

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