

# Road Effects on a Fire Salamander Population (*Salamandra salamandra terrestris*)

Diploma Thesis  
of  
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### **Abstract**

Amphibians are declining worldwide. There are many different causes for this global phenomenon. Traffic mortality is one of the reasons and is known that it can lead to local extinction. In my study I investigated effects of roadkills on abundance and age structure of a fire salamander population (*Salamandra salamandra terrestris*). I analysed the pattern of small scale distribution of salamanders on webs and determined age structure of the population with skeletochronology on toe clips. I compared data of two similar valleys situated next to each other; one of the valleys was dissected by a road. Between the valleys, I did not find a clear road effect on abundance of fire salamanders because of high variation within the valleysides and valleys. Within the valley with a road, I found fewer salamanders on the valley side with a road than on the side without road. Further, salamanders in the valley with a road were younger than salamanders in the valley without road. When analysing age structure separated by sex, I found the same effect in males, but not in females. The higher effect on males could be due to a higher activity level and migration activity during the long mating period. Further, males probably frequent plane structures to prospect for females and are therefore more vulnerable to get roadkilled. Thus, population structure was affected by the presence of a road and road effects will probably increase in future when traffic continues to increase.

## Introduction

Amphibians are declining world-wide (Barinaga 1990, Blaustein & Wake 1990, Alford & Richards 1999; Stuart et al. 2004). There are many different complex causes for this global phenomenon, some of them local and others more global. Ultraviolet radiation, predation, habitat modification, acidity and toxicants, diseases, changes in climate or weather patterns and interactions among the environmental factors can all lead to population declines (Alford & Richards 1999). Local density of amphibians can also be significantly negatively affected by traffic mortality (Van Gelder 1973; Fahrig et al. 1995; Lodé 2000). Many amphibians use different habitats during their annual cycle. When changing habitats, for example while migrating to the breeding sites, amphibians often must cross roads. Frequently, many of the roadcrossing animals are killed by vehicles. Van Gelder (1973) showed that at least 30% of females of *Bufo bufo* from the study population died in one season, while migrating to and back from breeding ponds, when traffic volume is only about 10 cars per hour in the evening. Carr & Fahrig (2001) also provided evidence that traffic mortality can cause population declines and they showed that more vagile species may be more vulnerable to road mortality than less vagile species. Ashley & Robinson (1996) recorded mortality on road from spring to autumn during two years. Recorded mortality exceeded 32'000 individuals, 30'034 thereof were Amphibians. Further, Fahrig et al. (1995) showed that in similar habitats frog and toad densities decreased with increasing traffic volume. About 40 years ago, first observations of amphibian massacres on roads were made in Switzerland (Meisterhans & Heusser 1970; Grossenbacher 1985). Since then, traffic volume has increased markedly throughout the world in the past two decades (United Nations, 1992). In Switzerland, traffic performance became nearly twice as high as in 1970 (Bundesamt für Raumentwicklung 2004). So, in the future the problem of amphibians killed by cars will probably become more significant.

Fire salamanders (*Salamandra salamandra*) are common in large parts of Central Europe, North Africa, Asia Minor, Israel and Iran (Thiesmeier 1992). The two most important habitats for fire salamanders are humid mixed deciduous forests for juvenile and adult animals, and spring-fed (summer cold) breeding streams for the larvae (Thiesmeier 1992). Therefore, females have to migrate from their terrestrial habitat to the stream to give birth to the larvae (mating is terrestrial). If there is a road between terrestrial habitat and stream, females have to cross the road to reproduce and run the risk of being killed by cars. Klewen (1985) describes, that fire salamanders actively frequent roads in the habitat. Different observations indicate that males may prefer plane structures like roads because there they have a good place to look for females. Thus, they rest on the road and the risk to get roadkilled increases. Furthermore, recently metamorphosed salamanders often need to cross the road to reach

the terrestrial habitat and while wandering around to find free territories. After an intense thundershower, Klewen (1985) counted 198 dead fire salamanders on a road with a low traffic volume. Adventitously, Schröder (1994) examined vertebrate mortality on two roads in Germany. 55.2% of roadkilled animals were amphibians, 25% therefrom were fire salamanders. Roadkilled salamanders can be found easily on almost any forest road.

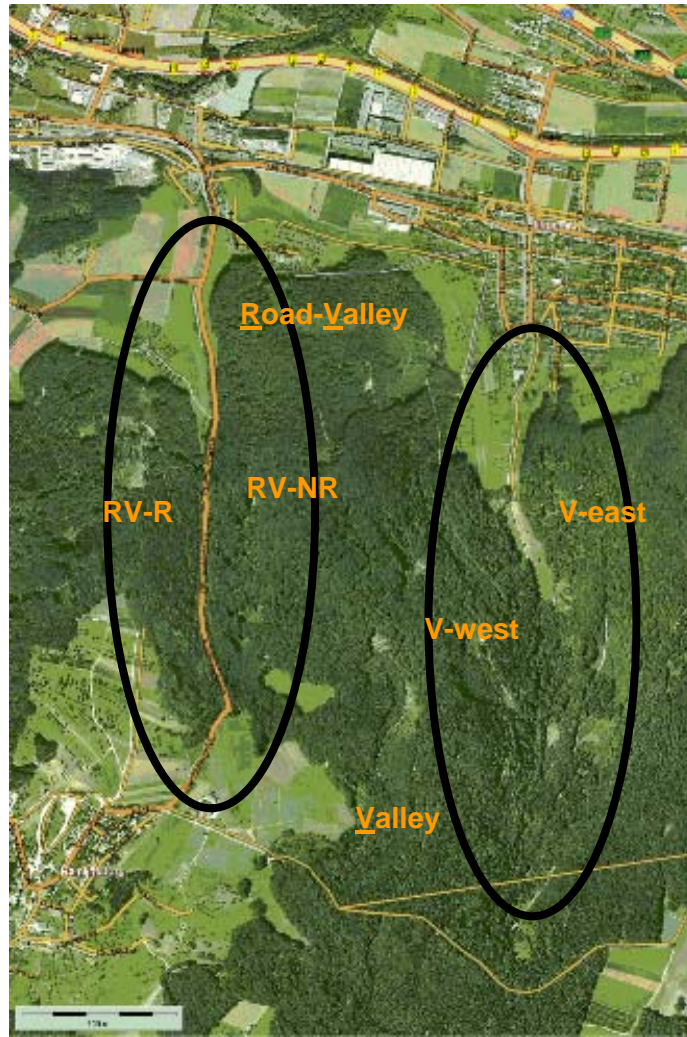
Road mortality, and therefore an increased mortality of adult salamanders is likely to have negative effects on salamander populations. Like in other long-lived animals, population growth rate is most sensitive to adult survival whereas recruitment plays a minor role (Schmidt et al 2005). In several amphibian species, the terrestrial juvenile and adult life-history stages are most important for population dynamics. Biek et al. (2002) described that in *Rana aurora* and *Rana temporaria* post-metamorphic vital rates and highly variable vital rates had a strong influence on the population dynamics. Vonesh & De la Cruz (2002) showed that for a range of density dependence scenarios population growth rates of *Bufo boreas* and *Ambystoma macrodactylum* were more sensitive to changes in post-embryonic survival parameters, particularly juvenile survival, than to egg survival. This suggests that mortality of terrestrial stages may play an important role in driving declines. Therefore, conservation biology studies should focus more intensively on the life-history stages which are most important for population growth.

In my study I investigated road effects on fire salamanders. I wanted to evaluate differences in abundance of fire salamander populations in two similar valleys, one of them crossed by a road with substantial traffic. Furthermore I assessed age structure of the populations and of the roadkilled animals.

### **Study Site**

My study sites were two small valleys southeast of Liestal in Canton Baselland, Switzerland (Fig. 1). The valleys are next and parallel to each other. Fire salamanders live in both valleys. In each valley, there is a small stream which serves as breeding habitat and runs from south to north. In the western valley, a road runs parallel to the stream (Fig. 2). Therefore, female salamanders of the western valleyside must cross the road when migrating to the stream to deposit larvae. Dead salamanders were regularly found on that road. In the other valley, there is also a small road. However, it is not a through road and is not often used in the evening and at night when salamanders are active. I never found any death salamanders on this road (in fact, there is a ban on driving on that road).

Hereafter, I will call the western valley with road RV (Road Valley), the western side which is traversed by the road side RV-R (Road Valley-Road), the eastern side RV-NR (Road Valley-No Road). The eastern valley without road is valley (V), with the sides V-east and V-west (Fig. 1). This geography of the study site allowed making two kinds of comparisons: within- and between valleys. Salamanders use relatively small home ranges and they are therefore unlikely to switch between valleys or the east and west sides within a valley (Feldmann 1966; Joly 1963/1968; Catenazzi 1998).



**Figure 1** Aerial photo of the study site with the two parallel valleys.



**Figure 2** Photograph of the road in RV-R



## **Hypotheses**

### ***Abundance***

*Within valleys:* In valley RV I expected to find a difference in abundance between the sides RV-R and RV-NR (density RV-R < RV-NR). This difference is caused by the loss of roadkilled animals. In valley V I did not expect a difference in density between east and west side because there is no obvious factor that could cause differential mortality.

*Between valleys:* I expected to find the highest population densities in sides V-east and V-west, a lower density in side RV-NR and the lowest density in side RV-R. The lower density in side RV-NR than in sides of valley V I expected because of a lower density of larvae in the stream. Because of the limited population density in side RV-R, there will be fewer larvae in the stream. Metamorphosed larvae disperse randomly to both valleysides. Thus, RV-NR is likely to be affected indirectly by traffic mortality in RV-R.

### ***Age Structure***

*Within valleys:* Age structure from side RV-R should have differed from the age structures in RV-NR, if animals in RV-R die younger because of the higher mortality risk on the road. Mean age in side RV-R was expected to be less than in side RV-NR. In valley V no difference between left and right side was expected.

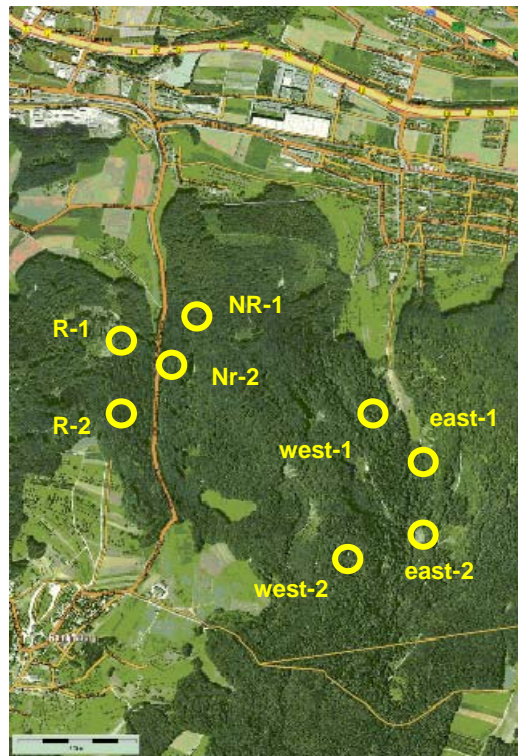
*Between valleys:* I expected the same age structure and age mean in side RV-NR like in sides of valley V.



## **Materials and Methods**

### ***Estimating Abundance: Field Methods***

To estimate population size I randomly chose two study areas on each valleyside where I established trapping webs, according to the distance sampling method with trapping webs (Buckland et al. 2001). Trapping webs are generally recommended for estimating abundance (Parmenter et al. 2003). I defined the centre “0” of the web and marked 8 radial lines, each 25m long. Instead of traps, I put small bamboo flags every  $2\frac{1}{2}$  meters, numbered from 1 to 10 (Fig. 4/5). There were two webs on each valleyside, altogether 8, each of them 50 meters in diameter and with 80 web sectors (Fig. 3).



**Figure 3** Locations and names of the eight webs.

For the analysis I also included salamanders I found within  $2\frac{1}{2}$  meters outside of the web and analyzed data therefore with 88 web sectors.

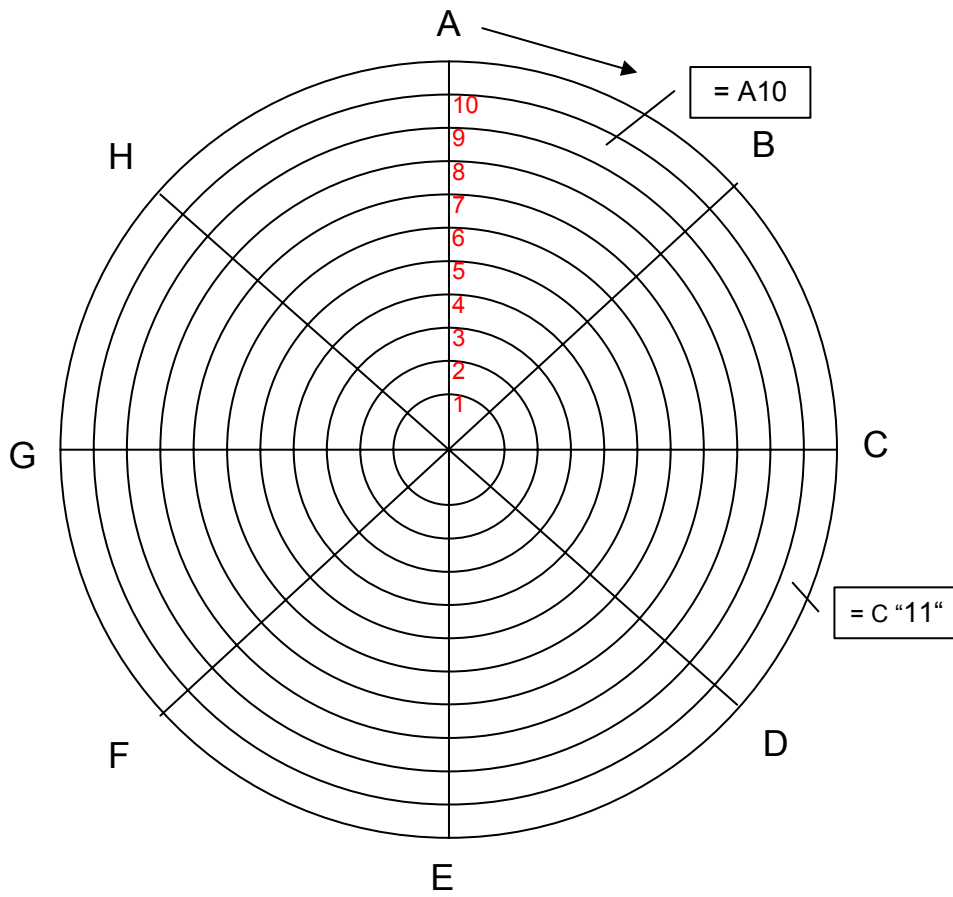


Figure 4 Schema of trapping webs.

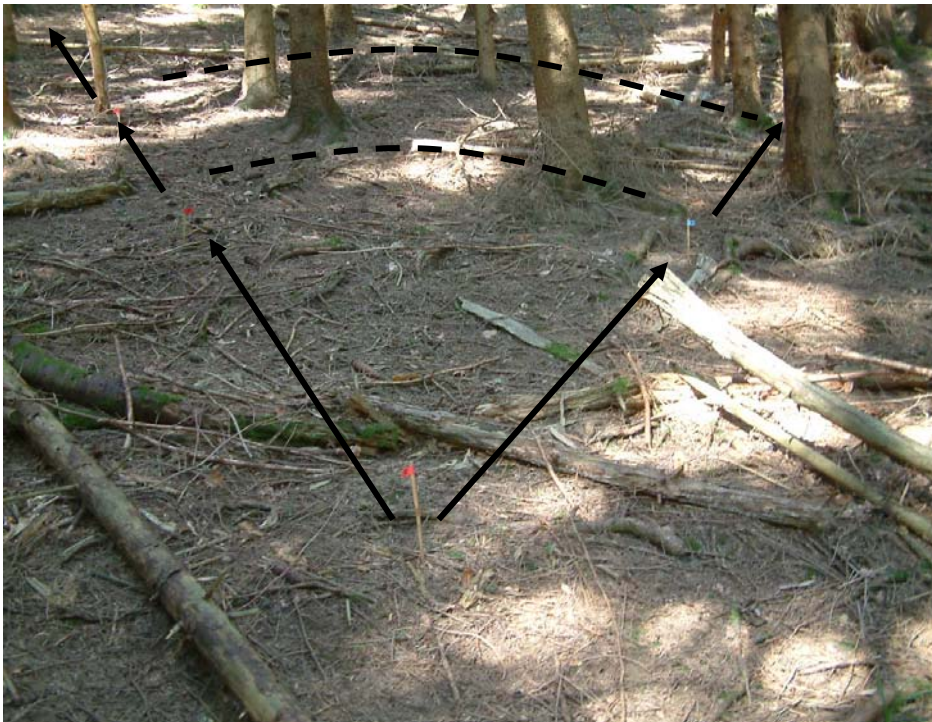


Figure 5 Photograph of trapping web west-2 with bamboo flags. Lines show web sectors according to figure 4.

I started fieldwork in May 2004. Each trapping web was searched for salamanders at least seven times until the end of August 2004 (Tab. 1).

**Table 1** Plan of the fieldwork.

web date	NR-1	NR-2	R-1	R-2	east-1	east-2	west-1	west-2
01.05.2004	x	x						
04.05.2004	x	x						
05.05.2004	x	x						
06.05.2004	x	x						
10.05.2004			x	x				
22.05.2004							x	
27.05.2004					x	x	x	x
31.05.2004	x	x	x					
01.06.2004					x	x	x	x
02.06.2004					x	x	x	x
11.06.2004	x	x	x	x				
13.06.2004	x	x	x	x				
20.06.2004					x	x	x	x
22.06.2004					x	x	x	x
06.07.2004	x	x	x	x				
08.07.2004			x	x	x		x	
13.07.2004			x	x				
21.07.2004						x	x	x
17.08.2004					x	x	x	x
19.08.2004	x	x	x	x				
24.08.2004	x	x		x				
26.08.2004			x	x	x		x	
Number of visits	10	10	9	9	8	7	10	7

Fieldwork started after 9pm when weather conditions were favourable for observing salamanders (wet, not windy). I always had someone coming and working with me. We walked along the radial lines of the webs and looked for fire salamanders with flash lights and a night vision scope. When we found a salamander, I noted exactly the place where it was found and its sex. The criterion for sex was the difference in the appearance of the cloacae. Cloacae of males are tumid, those of females are plane. Then I took a picture of the animal beside a size scale (Fig. 6). The pattern of yellow spots of each animal is unique (Feldmann 1967). Therefore I was able to recognize individuals when I recaptured one. Finally, I released the salamander at the place where it was found.



**Figure 6** Photograph of salamander with individual code and size scale as I took of each individual.

After field work had ended and before removing flags, I collected environmental factors of the webs. I counted number of deciduous trees and conifers in each web sector. I also noticed in categories of 0, 1, 2 or 3 scores for each of the following covariates: understorey, ground vegetation, deadwood and leaves. 0 for example meant no leaves, ground vegetation or deadwood respectively. Furthermore, I described the ground of each sector (humus layer or stones).

From MeteoSwiss I got meteorological data measured at the meteorological station Basel-Binningen, the meteorological station closest to my study sites. For my analysis I used the following data: rainfall on the sampling day, rainfall in the evening, mean air humidity in the evening, mean temperature in the evening and mean wind speed in the evening.

### ***Estimating Abundance: Statistical Analysis***

Because of relatively few captures, I could not use the distance-sampling-method and capture-recapture-analysis as I had planned. Distance sampling methods work well if more than 40 individuals are detected; this was not the case on most webs. Instead, I analysed the pattern of small-scale distribution of the salamanders on the trapping webs. That is, I estimated the proportion of sectors of the trapping webs were salamanders occurred. If abundance is high, then a large proportion of the sectors should be occupied whereas a small proportion of sectors should be occupied if abundance is low.

I estimated the proportion of sectors of the trapping web occupied by salamanders using the methodology outlined by MacKenzie *et al.* (2002) using the program PRESENCE v. 1 (available for download at <http://www.mbr-pwrc.usgs.gov/software.html>). MacKenzie *et al.* (2002) developed a likelihood-based method to estimate proportion of sites occupied by a species when detection probability is less than 1. The data for each site is recorded as a vector of 1's and 0's denoting detection and nondetection, respectively. It is possible to formulate a likelihood for every "detection history". For example, the likelihood for site  $i$  with detection history 01010 would be

$$\psi_i(1 - p_{i1})p_{i2}(1 - p_{i3})p_{i4}(1 - p_{i5})$$

$\psi_i$  is the probability that salamanders are present at site  $i$  and  $p_{it}$  the probability that salamanders will be detected at site  $i$  at time  $t$ , given presence. Assuming independence of the sites, the product of all terms, one for each site, constructed in this manner creates the model likelihood for the observed set of data, which can be maximized to obtain maximum likelihood estimates of the parameters. If  $\psi_i$  and  $p_{it}$  are constant across monitoring sites, the combined model likelihood can be written as

$$L(\psi, p) = \left[ \psi^n \prod_{t=1}^T p_t^{n_t} (1 - p_t)^{n - n_t} \right] \times \left[ \psi \prod_{t=1}^T (1 - p_t) + (1 - \psi) \right]^{N-n}$$

$N$  is the total number of surveyed sites,  $T$  the number of distinct sampling occasions,  $n_t$  the number of sites where salamanders were detected at time  $t$  and  $n$  the total number of sites at which salamanders were detected at least once. Standard deviation of  $\psi$  is estimated by a nonparametric bootstrap method. The estimation method makes these assumptions: Sites are occupied by salamanders for the duration of the survey period, with no new sites becoming occupied after surveying has begun, and no sites abandoned before the cessation of surveying (closed population). Salamanders are never falsely detected at a site when absent, and salamanders may or may not be detected at a site when present.

Covariate information like habitat type, habitat size or weather conditions can be easily introduced to the model using a logistic model for  $\psi$  and/or  $p$ . Because  $\psi$  does not change over time during the period of sampling (by assumption), appropriate covariates (1) would be constant and site specific, whereas covariates for detection probabilities (2) could be time varying and site specific. For my analysis I used the following covariates: (1) site covariates: number of deciduous trees, number of conifers, understory, ground vegetation, deadwood, leaves, sector size, web, valleyside, valley; (2) sampling covariates: rain day, rain evening,

mean air humidity evening, mean windspeed evening, mean temperature evening, sector size, date index. The algorithm that is used by program PRESENCE to search for the maximum of the likelihood function works best if values of the covariates are close to zero. Therefore, values of following covariates were divided by the factors given in the square brackets: sector size [ $\cdot 0.001$ ], air humidity [ $\cdot 0.001$ ], windspeed [ $\cdot 0.01$ ], temperature [ $\cdot 0.01$ ] and sector size [ $\cdot 0.001$ ]. For the date index, I set the first fieldnight as one and numbered days serially until the last fieldnight. This date index was used to model possible seasonal differences. To compare models with different covariates I used the AIC (Akaike's information criterion), calculated by PRESENCE:

$$AIC = -2\log(L(\psi, p) + 2K$$

where  $L$  is the likelihood,  $\psi$  the proportion of sites occupied,  $p$  the detection probability and  $K$  the number of estimated parameters in the model (Burnham & Anderson 2002). Furthermore, Akaike weight indicates the relative support of a model (Burnham & Anderson 2002):

$$w_i = \frac{\exp\left[-\left(\frac{\Delta AIC_i}{2}\right)\right]}{\sum \exp\left[-\left(\frac{\Delta AIC_i}{2}\right)\right]}$$

with

$$\Delta AIC_i = AIC_i - AIC_{\min}$$

$AIC_{\min}$  is the lowest AIC-value of the candidate models (i.e, the best model).

I used the following strategy for model selection:

1. With total data I looked for covariates which describe  $p$  best. This step serves to model detection probability adequately such that site occupancy and hypothesis tests can be done in the further steps.
2. I then checked which 'habitat covariates' describe  $\psi$  best. This step serves to account for variation in abundance among webs that is explained by variation in habitat quality. Once this variation is controlled for, the hypotheses (i.e. does the presence of the road affect abundance?) can be tested.
3. Including these covariates for  $p$  and  $\psi$ , I tested my hypotheses (covariates were web, valley side and valley).



To look for differences within valleys, I did step 3 also separately for both valleys. To do so, I used the same covariates as in the modelling of total data. If this was not possible because PRESENCE was not able to reach convergence, I included an additional covariate. This covariate was supposed to have little influence on the modelling of  $\psi$  and tests of the hypotheses, but should guarantee that convergence is reached.

To determine how the single webs were occupied, I calculated  $\psi$  for each web. Therefore I calculated means of scores  $x_c$  of the covariates (c) for each web. I then calculated  $\psi$  of location covariates in the weighted models (i.e. web or valleyside) and merged them relative to the Akaike weight of the model.

$$\psi = \frac{\exp(\text{int} + \sum x_c * \text{slope}(c))}{(1 + \exp(\text{int} + \sum x_c * \text{slope}(c)))}$$

### ***Estimating Age Structure: Laboratory Methods***

To determine age structure of the salamander (sub-)populations inhabiting each valleyside, I used the method of skeletochronology (Castanet et al., 1977; Castanet & Smirina 1990; Miaud 2001). When a salamander was encountered for the first time, I clipped the fourth hind leg toe and stored it in 96% EtOH until use. I used sections of the diaphysis of toe phalanx to count the lines of arrested growth (LAG). To get a bigger sample size, I also included toes clipped from salamanders I found on the way to the webs. Furthermore I collected dead salamanders on the road and also used one toe of them. In the lab, I removed skin, muscles and sinews from the phalanx. If the third phalanx was intact, I used the third, otherwise the second phalanx. I then washed the bones for one hour in bidistilled water. Afterwards I decalcified them in 3% nitric acid for 4<sup>1</sup>/<sub>2</sub> hours. Then I washed the bones in tap water overnight. I made 14 $\mu$ m thin cross sections from the diaphyseal region using a freezing microtome. As embedding material I used SAKURA Tissue-Tek (Haslab GmbH, Switzerland) and to minimize loss of sections while staining I used SuperFrost<sup>®</sup>Plus (Menzel GmbH & Co) microscope slides. Sections were stained with Ehrlich's haematoxylin and mounted with Aquatex (MERCK (Schweiz) AG). I observed sections with a light microscope and to minimize reading error, I examined multiple sections of each sample and adjusted light and focus accordingly. I repeated the count of each sample to avoid differences from the first to the last count.



### ***Estimating Age Structure: Statistical Analysis***

To determine if there is an impact of the road on the age structure of the salamander population living on the road side of the valley, I tested for age differences between valleysides and valleys and for interactions. For this analysis, I included data of roadkilled animals in data of animals living on the road side. To test more specifically my hypotheses, I did comparisons between age-data of single valleysides and valleys, I used an analysis of contrasts in the SAS procedure for general linear models (GLM; SAS Institute Inc. 2001). Because the sex of roadkilled salamanders could not be determined anymore, this analysis did not include the factor "sex" which would have allowed testing for sex-specific effects of traffic mortality on age structure. To test for an effect of sex, I redid the analysis separately for each sex and excluded roadkilled salamanders. Those analyses I did with a general linear model using the procedure GLM in program SAS (SAS Institute Inc. 2001). Again I tested my hypotheses with the option contrast in SAS separately by sex.

**Results**

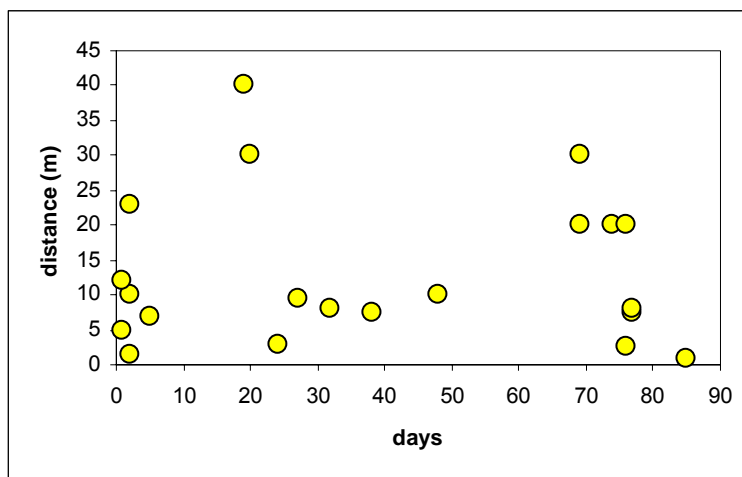
***Salamander Captures***

During my field season, I totally captured 292 salamanders (inclusive recaptures). Numbers of salamanders I captured on each day and on each web are shown in Tab. 2.

**Table 2** Number of salamanders captured.

web date	NR-1	NR-2	R-1	R-2	east-1	east-2	west-1	west-2	not on webs	total
01.05.04	2	4							24	30
02.05.04									8	8
04.05.04	0	3							1	4
05.05.04	4	2							2	8
06.05.04	2	3								5
10.05.04			0	1					4	5
22.05.04							0		6	6
27.05.04					1	4	0	2	23	30
31.05.04	3	5	1						1	10
01.06.04					3	8	5	13	2	31
02.06.04					1	7	1	5	2	16
11.06.04	11	4	3	8						26
13.06.04	6	5	0	5						16
20.06.04					1	3	0	1		5
22.06.04					1	1	0	1		3
06.07.04	3	0	0	0						3
08.07.04			3	7	2		1			13
13.07.04			0	6						6
21.07.04						0	0	4		4
17.08.04					4	7	1	4		16
19.08.04	12	12	0	1						25
24.08.04	6	6		3						15
26.08.04			1	5	0		1			7
total	49	44	8	36	13	30	9	30	73	292

Photos of captured salamanders I compared with photos of previous captured salamanders. Recaptures of individually known salamanders allowed to estimate the mean distance between first and second captures (I never recaptured an individual more than twice). Mean distance from first to second capture was about 13 meters; thus, individuals occupy multiple sectors on a trapping web. Further, recaptures were always found within the same web as in the first capture. Time between captures had no influence on distance (GLM, n=21, p=0.95) (Tab. 4, Fig. 7), but there was a difference between sexes (p=0.046). Juvenile salamanders I found, on average, 6 meters from the first capture place, males 11 and females 22 meters from the first capture place (Tab. 3).



**Figure 7** Distance between first capture and recapture of an individual in relation to time between the captures.

**Table 3** Mean distance and mean time between recaptures.

sex	distance (m)	time (d)
j (n = 3)	6	24
m (n = 13)	11	39
f (n = 5)	22	48

**Table 4** Analysis of factors affecting distance between captures.

Source (n=21)	df	ss III	ms	f	P
time	1	0.37	0.37	0.00	0.951
sex	2	712.42	712.42	3.82	<b>0.046</b>
time*sex	2	225.00	225.00	1.21	0.327
residual	15	1399.69	93.31		

### Abundance

In my modelling I first looked for covariates which described  $p$  (probability that salamanders will be detected) best. The best model included the covariates were 'rain day', 'rain evening', and 'air humidity' (Tab. 5).

**Table 5** Model selection to determine which sampling covariates best describe detection probabilities of salamanders. For this analysis, site occupancy was held constant (i.e.  $\psi(\cdot) \rho(\text{covariates})$ ). Shown are models with an Akaike weight > 0.05.

model	AIC	$\Delta$ AIC	w
<b><math>p(\text{rain day, rain evening, air humidity})</math></b>	1730.31	0.00	<b>0.281</b>
$p(\text{rain day, rain evening, air humidity, size})$	1731.66	1.35	0.143
$p(\text{rain day, rain evening, air humidity, temperature})$	1731.80	1.48	0.134
$p(\text{rain day, rain evening, air humidity, date index})$	1732.29	1.98	0.104
$p(\text{rain day, rain evening, air humidity, wind})$	1732.31	2.00	0.103
$p(\text{rain day, rain evening, air humidity, temperature, size})$	1733.15	2.84	0.068
$p(\text{rain day, rain evening, air humidity, temperature, date index})$	1733.43	3.11	0.059
$p(\text{rain day, rain evening, air humidity, size, date index})$	1733.64	3.33	0.053
$p(\text{rain day, rain evening, air humidity, wind, size})$	1733.66	3.35	0.053

$\Delta$ AIC is the difference between the model with the lowest AIC and the given model and w is the Akaike weight.

The second step in the analysis was to identify the habitat covariates that best explain site occupancy.  $\psi$  (overall proportion of sites occupied) was best described by a model that included the covariates ‘understorey’, ‘deadwood’ and ‘size’ (Tab. 6).

**Table 6** Model selection to determine which site covariates best describe abundance of salamanders. For this analysis best sampling covariates (sampling cov.) were used ( $\rho$ (rain day, rain evening, air humidity)). Shown are models with an Akaike weight > 0.05.

model	AIC	$\Delta$ AIC	w
$\psi$ (understorey, deadwood, size) $\rho$ (sampling cov.)	1716.50	0.00	<b>0.286</b>
$\psi$ (understorey, deadwood, size, leaves) $\rho$ (sampling cov.)	1717.94	1.44	0.139
$\psi$ (understorey, size) $\rho$ (sampling cov.)	1718.25	1.74	0.120
$\psi$ (understorey, deadwood, size, ground vegetation) $\rho$ (sampling cov.)	1718.25	1.74	0.120
$\psi$ (understorey, deadwood) $\rho$ (sampling cov.)	1718.82	2.32	0.090
$\psi$ (understorey, size, ground vegetation) $\rho$ (sampling cov.)	1719.38	2.88	0.068
$\psi$ (understorey, size, leaves) $\rho$ (sampling cov.)	1719.52	3.02	0.063
$\psi$ (understorey, deadwood, leaves) $\rho$ (sampling cov.)	1719.67	3.17	0.059
$\psi$ (understorey, deadwood, size, leaves, ground vegetation) $\rho$ (sampling cov.)	1719.76	3.26	0.056

$\Delta$ AIC is the difference between the model with the lowest AIC and the given model and w is the Akaike weight

These covariates serve to statistically remove all the variation in site occupancy among webs that is due to variation in habitat quality. These covariates thus allow testing the hypotheses of a road effect (with covariates ‘web’, ‘valleyside’ or ‘valley’) without confounding effects of variation in habitat quality. Including data from both valleys, the model selection analysis that compared these competing hypotheses showed that the model with the lowest AIC was  $\psi$ (understorey, deadwood, size, web) $\rho$ (rain day, rain evening, air humidity). Akaike weight of this model was 0.67, so abundance was best explained by variation among webs. The model with covariate valleyside also got some support from the data with an Akaike weight of 0.33. The other two models had an Akaike weight of 0 (Tab. 7). It is noteworthy that model  $\psi$ (understorey, deadwood, size) $\rho$ (rain day, rain evening, air humidity) had no support from the data in this analysis at all even though it was the best model as determined in the first two steps of the analysis. This implies that habitat covariates alone apparently do not adequately describe spatial variation in abundance.

**Table 7** Ranking of models with total data.

rank	model	AIC	$\Delta$ AIC	w	$\psi$	SE( $\psi$ )
1	$\psi$ (understorey, deadwood, size, <b>web</b> ) $\rho$ (rain day, rain evening, air humidity)	1695.70	0.00	0.67	0.560	0.067
2	$\psi$ (understorey, deadwood, size, <b>valleyside</b> ) $\rho$ (rain day, rain evening, air humidity)	1697.16	1.46	0.33	0.578	0.071
3	$\psi$ (understorey, deadwood, size, <b>valley</b> ) $\rho$ (rain day, rain evening, air humidity)	1710.94	15.24	0.00	0.526	0.063
4	$\psi$ (understorey, deadwood, size) $\rho$ (rain day, rain evening, air humidity)	1716.51	20.80	0.00	0.543	0.064

$\Delta$ AIC is the difference between the model with the lowest AIC and the given model, w is the Akaike weight,  $\psi$  is the estimated proportion of sites occupied and SE ( $\psi$ ) the standard error thereof.

In Table 8 and 9 estimates of the slopes (and standard errors) of the covariates of the two best models are shown. A positive slope for example means that the covariate influences detectability or presence positively. For example, in my model the higher the air humidity is the more fire salamanders will be detected. However, covariates are measured on different scales, hence a larger slope does not imply that a covariate has a stronger effect than a covariate with a smaller slope.

**Table 8** Slopes and standard errors of covariates on the logit scale) from the best model.

covariate	slope	standard error
$\psi$		
intercept	-0.056	0.753
NR-2	1.074	1.201
R-1	-1.730	1.119
R-2	-0.872	0.834
east-1	-1.492	0.790
east-2	-0.475	0.959
west-1	-2.013	0.858
west-2	-0.165	1.013
understorey	-0.593	0.389
deadwood	0.444	0.289
size	32.448	15.802
$\rho$		
intercept	-6.910	1.062
rain day	3.882	1.853
rain evening	-5.437	1.892
air humidity	46.033	13.068

**Table 9** Slopes and standard errors of covariates (on the logit scale) from the second best model.

covariate	slope	standard error
$\psi$		
R	-2.655	1.055
east	-2.566	1.125
west	-2.777	1.121
intercept	1.425	1.157
understorey	-0.878	0.314
deadwood	0.604	0.294
size	32.023	16.397
$\rho$		
intercept	-7.083	1.084
rain day	3.432	1.837
rain evening	-4.685	1.865
air humidity	47.668	13.361

I also calculated  $\psi$  for each web. Mean values ( $x_c$ ) of the covariates (c) are shown in Tab. 10. To calculate  $\psi$  I used the means of the covariates used in my models ('size', 'understorey' and 'deadwood'). I then calculated  $\psi$  for the webs with the data of the models supported by the Akaike weight (model with location covariate web and model with location covariate valleyside, Tab. 7) and merged the results relative to the Akaike weight of the models. Results are shown in Tab. 11.

**Table 10** Number of trees and means ( $x_c$ ) of covariate scores in each web. Covariates used in the modelling are bold.

web/covariate	deciduous trees	conifers	<b>understorey</b>	ground vegetation	<b>deadwood</b>	<b>size</b>	leaves
NR-1	76	1	0.08	1.07	1.10	0.0268	1.77
NR-2	43	1	1.89	0.48	1.11	0.0268	1.41
R-1	26	1	1.97	0.17	1.22	0.0268	1.70
R-2	51	1	0.15	0.48	1.95	0.0268	2.50
east-1	43	34	0.36	1.17	0.73	0.0268	1.43
east-2	10	62	0.09	1.94	1.61	0.0268	0.19
west-1	68	15	0.85	0.88	0.88	0.0268	0.91
west-2	11	248	0.00	0.00	1.66	0.0268	0.17

**Table 11**  $\psi$ -estimates of webs and their means per valleyside.

valleyside web	RV-R		RV-NR		V-west		V-east	
	R-1	R-2	NR-1	NR-2	west-1	west-2	east-1	east-2
$\psi$	0.26	0.59	0.74	0.74	0.30	0.69	0.43	0.67
mean $\psi$ of the webs in one valleyside	0.43		0.74		0.50		0.55	

$\psi$  is the estimated overall proportion of sites occupied.

Web-specific estimates of  $\psi$  (Table 11) were highly correlated with the number of salamander captures on a web (Table 2):  $r=0.908$ ,  $P=0.0017$ .

To determine if abundance differs between the two sides of each valley, the analysis was also done separately for each valley. For calculating models in RV I also had to include covariate 'leaves'. Otherwise PRESENCE was not able to reach convergence. In valley RV, the best supported model was  $\psi(\text{understorey, deadwood, leaves, size, valleyside})p(\text{rain, rain evening, air humidity})$  with an Akaike weight of 0.7 (Tab. 12). Less support got the model including covariate web (Akaike weight 0.3). Within the road valley, valleyside was more important to describe the data than web-location. Furthermore, the model without a location covariate was bad, which corresponds to my hypotheses that valleyside is important to describe  $\psi$ .

**Table 12** Model ranking for RV.

rank	model	AIC	$\Delta$ AIC	w	$\psi$	SE( $\psi$ )
1	$\psi(\text{understorey, deadwood, leaves, size, } \mathbf{valleyside})$ $p(\text{rain day, rain evening, air humidity, size})$	1013.306	0.00	0.70	0.759	0.037
2	$\psi(\text{understorey, deadwood, leaves, size, } \mathbf{web})$ $p(\text{rain day, rain evening, air humidity, size})$	1014.988	1.68	0.30	0.702	0.050
3	$\psi(\text{understorey, deadwood, leaves, size})$ $p(\text{rain day, rain evening, air humidity, size})$	1033.918	20.61	0.00	0.618	0.130

In V road, the AIC values of the models were close to each other. Most support got the model without the location covariates ‘web’ or ‘valleyside’ and least support the model with location covariate valleyside (Tab. 13). That corresponds to my hypotheses that, in this valley, valleyside is not important to describe  $\psi$ .

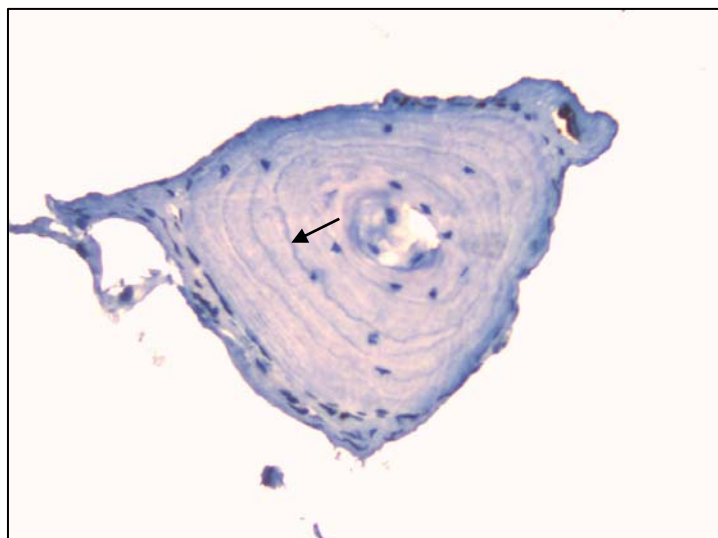
**Table 13** Model ranking for V.

rank	model	AIC	$\Delta$ AIC	w	$\psi$	SE( $\psi$ )
1	$\psi$ (understorey, deadwood, size) $\rho$ (rain day, rain evening, air humidity, size)	653.111	0.00	0.46	0.450	0.122
2	$\psi$ (understorey, deadwood, size, <b>web</b> ) $\rho$ (rain day, rain evening, air humidity, size)	653.510	0.40	0.37	0.485	0.137
3	$\psi$ (understorey, deadwood, size, <b>valleyside</b> ) $\rho$ (rain day, rain evening, air humidity, size)	655.110	2.00	0.17	0.449	0.125

The estimates of  $\psi$  can be used to calculate salamander density. Web area was 2376 m<sup>2</sup>, and if  $\psi$  is 0.5 there would be 44 salamanders per web (88 sectors (= sites),  $\psi$ =proportion of sites occupied). So density would be about 185 salamanders per hectare or one salamander per 54m<sup>2</sup>. In my study,  $\psi$  of valleysides are between 0.43 and 0.74 or densities between 159 and 274 salamanders per hectare.

### Age Structure

Toe clips of 224 salamanders were used for the analysis of the age structure of the salamander populations. In Fig. 8, a stained cross section of a five year old individual is shown.



**Figure 8** Cross section of a toe phalanx of a five year old individual, one lag (line of arrested growth) is marked with the arrow.



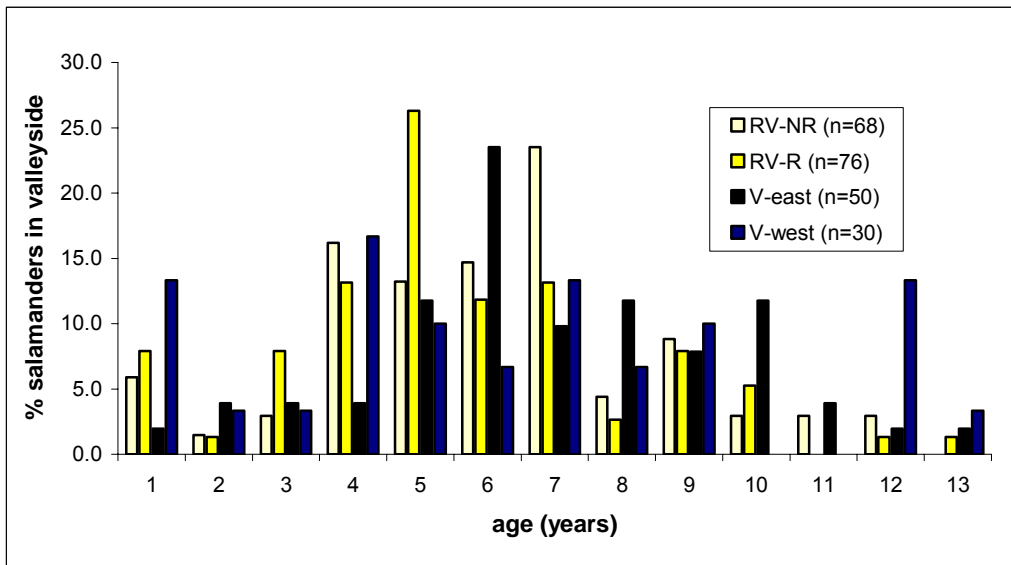


Figure 9 Age distribution of the salamanders on the different valleysides.

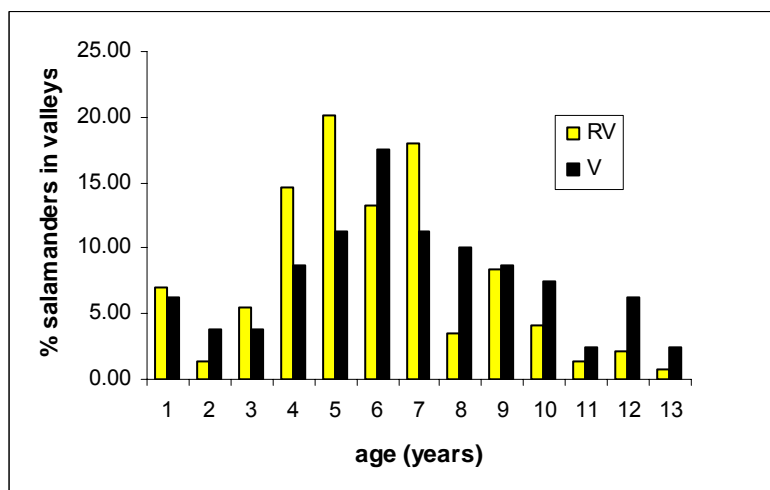


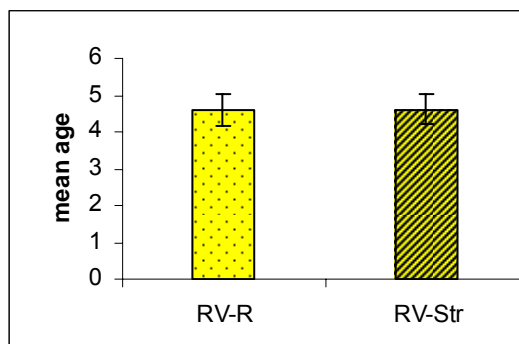
Figure 10 Age distribution in the two valleys.

Because it was not possible to sex juveniles or roadkilled salamanders, I performed two analyses.

- In the first analysis, I tested for differences in age of adult salamanders between valleys and valleysides. Here, roadkilled animals were included.
- In a second analysis, I tested whether differences in age of adult salamanders between valleys and valleysides depended on sex. Here, roadkilled salamanders were excluded.

Each analysis proceeded as follows. I first calculated an analysis of variance. Then I tested my hypotheses more specifically using contrast analysis. I included data of roadkilled

salamanders in data of valleyside RV-R. Before I did this, I tested for differences between mean age of roadkilled animals and mean age of animals in valleyside RV-R. There was no significant difference between them (n=76; F=0.00; P=0.965) (Fig. 11).



**Figure 11** Mean age and standard errors in RV-R and of roadkilled salamanders (RV-Str).

Kalezić et al. (2000) calculated average time of sexual maturity in *S. salamandra* with 3.4 years for males and with 3 years for females. For *Salamandra s. gallaica*, Rebelo & Caetano (1995) indicate sexual maturity for males with 2-3 years and for females with 3-4 years. Thus, I excluded one and two year old juveniles from the analysis.

In the first analysis, salamanders in V were significantly older than salamanders in RV. There was no significant age difference between the valleysides and the interaction was also not significant (Tab. 14).

**Table 14** Analysis of age data of adult salamanders, inclusive roadkilled animals (excluding variable sex).

source (n=205)	df	ss III	ms	f	P
valley (RV-V)	1	50.70	50.70	8.80	<b>0.003</b>
side (east-sides-west-sides)	1	4.46	4.46	0.77	0.380
valley*side	1	1.14	1.14	0.20	0.657
residual	201	1157.44	5.76		

I then tested specific hypotheses using contrast analysis (Tab. 15) and calculated mean ages of each valleyside (Tab. 16). Salamanders in RV-R were significantly younger than salamanders in the other three sides and than salamanders in V. Also salamanders in RV-NR were significantly younger than salamanders in V. There was no difference between the sides within valleys.

**Table 15** Results of contrast analysis: Comparisons of ages among valleysides and valleys of adult salamanders inclusive roadkills.

source (n=205)	df	ss III	ms	f	P
RV-R vs. RV-NR <sup>1</sup>	1	7.60	7.60	1.32	0.252
V-east vs. V-west <sup>2</sup>	1	0.41	0.41	0.07	0.790
RV-R vs. others <sup>3</sup>	1	46.72	46.72	8.11	<b>0.005</b>
RV-R vs. V <sup>4</sup>	1	58.25	58.25	10.11	<b>0.002</b>
RV-NR vs. V <sup>5</sup>	1	22.43	22.43	3.90	<b>0.0498</b>

1 This contrast asks whether age differs between the two valleysides in valley RV.

2 This contrast asks whether age differs between the two valleysides in valley V.

3 This contrast asks whether age in RV-R differs from the other three sides.

4 This contrast asks whether age in RV-R differs from age in valley V.

5 This contrast asks whether age in RV-NR differs from age in valley V.

**Table 16** Mean ages of adult salamanders, inclusive roadkilled salamanders.

valleyside	mean age	se	n
RV-R	6.04	0.27	69
RV-NR	6.52	0.27	63
V-east	7.44	0.37	48
V-west	7.28	0.61	25

In the second analysis, where I analysed the data separated by sex, there was a significant difference between mean ages of males between the valleys. There was an age difference in males between the two valleys. In females there was no difference between locations (Tab. 17).

**Table 17** Analysis of age data, separated by sex, exclusive 1 and 2 year old salamanders (exclusive roadkilled salamanders).

source	df	ss III	ms	f	P
<i>males (n=104)</i>					
valley (RV-V)	1	34.20	34.20	5.07	<b>0.027</b>
side (east-sides-west-sides)	1	9.08	9.08	1.35	0.249
valley*side	1	0.02	0.02	0.00	0.956
residual	100	674.26	6.74		
<i>females (n=66)</i>					
valley (RV-V)	1	0.69	0.69	0.15	0.701
side (east-sides-west-sides)	1	0.05	0.05	0.01	0.917
valley*side	1	1.11	1.11	0.24	0.625
residual	62	286.08	4.61		

I tested my hypotheses using contrast analysis separated by sex and calculated mean ages of males and females in each valleyside (Tab. 18/19). Males in RV-R were significantly

younger than males in V. Between sides within valleys there was no significant difference. In females there were again no significant differences between locations.

**Table 18** Comparisons of sites, separated by sex, exclusive 1 and 2 year old salamanders (exclusive roadkilled salamanders).

source	df	ss III	ms	f	P
<i>males (n=104)</i>					
RV-R vs. RV-NR <sup>1</sup>	1	4.63	4.63	0.69	0.409
V-east vs. V-west <sup>2</sup>	1	4.46	4.46	0.66	0.418
RV-R vs. others <sup>3</sup>	1	22.53	22.53	3.34	0.071
RV-NR vs. V <sup>4</sup>	1	13.88	13.88	2.06	0.155
RV-R vs. V <sup>5</sup>	1	31.31	31.31	4.64	<b>0.034</b>
<i>females (n=66)</i>					
RV-R vs. RV-NR <sup>1</sup>	1	0.90	0.90	0.20	0.660
V-east vs. V-west <sup>2</sup>	1	0.51	0.51	0.11	0.742
RV-R vs. others <sup>3</sup>	1	1.34	1.34	0.29	0.593
RV-NR vs. V <sup>4</sup>	1	0.16	0.16	0.04	0.851
RV-R vs. V <sup>5</sup>	1	1.16	1.16	0.25	0.619

1 This contrast asks whether age differs between the two valleysides in valley RV.

2 This contrast asks whether age differs between the two valleysides in valley V.

3 This contrast asks whether age in RV-R differs from the other three valleysides.

4 This contrast asks whether age in RV-R differs from age in valley V.

5 This contrast asks whether age in RV-NR differs from age in valley V.

**Table 19** Mean ages of valleyside, separated by sex. Data exclusive roadkilled and one and two year old salamanders.

valleyside	mean age	se	n
<i>males</i>			
RV-NR	6.79	0.45	29
RV-R	6.16	0.50	19
V-east	7.94	0.44	34
V-west	7.36	0.67	22
<i>females</i>			
RV-NR	6.29	0.33	34
RV-R	6.00	0.64	15
V-east	6.21	0.59	14
V-west	6.67	1.45	3

## **Discussion**

Within the roadvalley, I found as expected, a higher abundance on the roadside than on the side without road. However, the overall proportion of sites occupied was higher in the roadvalley than in the valley without a road. Thus, within the valleys, a road effect was apparent, but not between the valleys. Further, as expected, salamanders in the roadvalley were younger than in the valley without a road but, contrary to my expectations, the effect was stronger in males than in females. Overall, my hypotheses were confirmed for the most part, but not as clearly as I had expected.

### ***Detection Probabilities***

**To detect fire salamanders it was most important that soil and air humidity was high.**

Detection probabilities of fire salamanders on trapping webs were best described by the covariates 'rain day', 'rain evening', and 'air humidity' whereas 'temperature', 'wind force', 'sector size', and 'date index' had no influence (Tab. 5). Salamanders could only be found if humidity of soil and air were high enough. Contrary to Thiesmeier (2004), who says that the three main factors affecting detectability of fire salamanders are temperature, humidity and wind force, in my study temperature and wind force had no important influence on detection probability. Wind force and humidity are probably correlated; if there is wind, humidity goes down. Further, if there was much rain during fieldwork in the evening, detection probability became lower.

### ***Abundance***

I use the proportion of sites occupied on the trapping webs ( $\psi$ ) as a surrogate for abundance (MacKenzie & Nichols 2004).

**Salamanders in my study ranged within small areas.**

Salamanders that I captured twice were recaptured about 13 meters away from the first capture place. The time between captures had no influence on distance (Fig. 7). As found in other studies, salamanders in my study moved within quite small distances (Joly 1963/1968, Klewen 1985) and I never recaptured a salamander on a different web. This supports my expectation that salamanders do not switch between the valleys and valleysides.

**Differences in habitat quality affected site occupancy of salamanders.**

To describe the abundance ( $\psi$ ) the most important habitat covariates were 'understorey', 'deadwood' and 'sector size' (Tab. 6). The amount of understorey had a negative effect on  $\psi$  whereas deadwood had a positive effect on abundance of fire salamanders. Fire salamanders use, among other things, deadwood as hiding places (Thiesmeier 2004). Thus, the positive effect of deadwood on abundance could be because salamanders use deadwood during daytime as hideout and therefore prefer areas with a high availability of deadwood. Sector size had a positive effect, as one would expect, the larger the sectors were the more likely a sector was occupied by salamanders. Including location covariates in the modelling, the best model was the model with the location covariate 'web'. Thus, web location *per se* played a major role in describing salamander abundance and there was high variation of  $\psi$  between the webs. Thus, the strong variation in site occupancy among trapping webs showed that salamanders are patchily distributed, even when statistically controlling for variation in habitat quality. The alternative models were less well supported (Tab. 7). Hence, the habitat variables I used in my study explain some abundance differences, but there must be additional variation among webs which can not be explained by the habitat covariates used in my analysis. Thiesmeier (2004) describes that fire salamanders often occur patchily in the habitat. There appear to exist core areas, often along breeding streams or within attractive habitat structures, where most salamanders occur (Thiesmeier 2004). Preferences for places near breeding streams I could not find in my study. Some webs near the breeding streams were less occupied (e.g. west-1,  $\psi = 0.30$ ), others near the stream were well occupied (e.g. NR-2,  $\psi = 0.74$ ). And also some webs far from the breeding stream were well occupied (e.g. R-2,  $\psi = 0.59$ ). Furthermore, fire salamanders use mainly burrows, stones, or deadwood as daily hiding places. As mentioned, availability of deadwood had a positive effect on abundance of fire salamanders. Therefore, availability of burrows and stones could also positively influence the distribution of fire salamanders within the habitat. Taub (1961) found that a large proportion of a Red-Backed Salamander population is distributed within the soil. Thus, if availability of burrows is high in an area, there is high availability of hiding places and more salamanders will probably occur there than in an area with few burrows. This would be congruent with the positive effect of availability of deadwood on abundance. Availability of burrows and large stones I did not investigate in my study and therefore not use it in my analysis. So, if availability of burrows or stones differs within the valleysides, the variation of abundance I found among webs occurs possibly due to this difference. Therefore, roads in the habitat and especially building of roads would probably have another negative effect on fire salamanders. Riley (1984) showed that road construction increases soil compaction up to 200 times. In such areas, availability of burrows probably decreases and as well habitat quality for fire salamanders would decrease.

**Valleyside had an influence on abundance of fire salamanders.**

The model with location covariate 'valleyside' was the second best model (Tab. 7). Thus, as I had expected due to the road, valleyside had an influence on salamander abundance. Taking the mean  $\psi$  of the two webs on one valleyside, the best occupied side was RV-NR. The lowest  $\psi$  was found in RV-R and a little higher  $\psi$  in V-west and V-east than in RV-R (Tab. 11).

Within the road valley, occupancy of salamanders was different between the two sides and a model including the covariate valleyside was the best model (Tab. 12). As expected in RV there was a higher abundance in RV-NR than in RV-R. This difference could be due to the increased mortality on the road. But also in RV-R there was high variation of  $\psi$  between the two webs with one good and one bad occupied web (Tab. 11). In RV-NR both webs were very well occupied. That makes it difficult to argue about a strong road effect. However, the  $\psi$  of both webs in RV-NR was higher than  $\psi$  of the good occupied web in RV-R. This is consistent with the hypotheses that there is a lower abundance in RV-R than in RV-NR due to the road. Between the valleys, I had expected to find a lower  $\psi$  in RV due to the many roadkills but overall site occupancy there was higher than V. Thus, a clear road effect on abundance between the valleys was not apparent. In valley V, site occupancy was determined primarily by habitat quality as neither the model with covariate valleyside nor web location was well supported. Also, in both of these two valleysides there was one well and one little occupied web. But in the modelling (Tab. 13), models with location covariates ('web' and 'valleyside') were less important than the model without any location covariate which means that, as expected in this valley, the valleyside plays a minor role to explain abundance.

**Within the valleys my hypotheses about abundance were confirmed for the most part, but due to high variation between the webs not as clearly as expected.**

In view of the many roadkilled salamanders one would expect clearer effects of the road on abundance of fire salamanders in RV-R and the road valley (RV) as a whole. There were nights when I found up to 20 roadkilled fire salamanders until 2 a.m. Possibly, there exists a density dependent regulation mechanism in adult fire salamanders and the population is able to compensate the loss of adults on the road. In amphibians, a lot of research has been done on density dependent regulation mechanisms in larvae (i.e. Petranka 1989, Scott 1994, Semlitsch 1982, Taylor & Scott 1997), but in adults, not much is known about such mechanisms. Altwegg (2003) found evidence for density-dependence in terrestrial juvenile frogs. Further, Meyer et al. (1998) found evidence for density dependent population regulation in *Rana temporaria*, but it is not clear in which stage of life cycles the density dependence occurs. However, Berven (1990) found that population size of wood frogs (*Rana*



*sylvatica*) negatively affected fecundity of females and therefore population is density regulated. An alternative explanation may be that traffic volume increased only recently and therefore an effect of road mortality may not yet be apparent.

### **Population density in both valleys was quite high.**

Taking means of  $\psi$  of the two webs in on side, lowest density found in RV-R was about 159 salamanders per hectare. Highest density found in RV-NR was about 274 salamanders per hectare. Compared to other studies (Klewen 1985, Thiesmeier 1990, Seifert 1991, Joly 1968, Denoel 1996), these are quite high densities. Therefore all valleysesides are well occupied by fire salamanders and, with the exception of the road, the valleys seem, except of the road, to be good habitats for fire salamanders. Such a high density suggests that density-dependent regulation of the population is not unlikely.

## ***Age structure***

### **Proportion of old salamanders in the road-valley (RV) was lower than in the valley without road (V).**

I found a shifted age distribution in the road valley in comparison to the other valley (Fig. 10). For example in RV only about 20% (total n=144) of the fire salamanders were 8 years and older and in V about 38% (total n=80) of salamanders were 8 years and older. Thus, salamanders in RV probably die younger than salamanders in V, consistent with the hypothesis of the increased mortality risk on the road.

### **Mean age of salamanders differed between the two valleys, as expected under the hypothesis of an effect of traffic on mortality.**

Mean age of salamanders in RV was lower than in V, but there was no difference between mean ages of the two valleysesides in RV; the effect is, however, only visible in males (Table 19, see also below). Thus, a road effect on mean age is evident in the comparison between valleys. However, and contrary to my hypotheses, also salamanders in RV-NR are younger than salamanders in V, so they probably are affected by road mortality as well. Therefore, salamanders must switch between the two valleysesides. In the lower part of RV, the road is very close to the stream and a wide, bridge-like forest track crosses the stream. It may be that RV-NR salamanders occasionally switch to the other side and get killed on the road. It may also be that a hibernation site used by RV-NR salamanders is located in RV-R (salamanders are known for the communal use of hibernation sites (Feldmann 1966)).

An alternative explanation that mean age of salamanders in V is higher than in RV could be that there is lower recruitment in V. But this explanation is unlikely, as I found about the same proportion of young salamanders in both valleys (Fig. 10). Further, microclimate may affect age structure. Reaser (2000) found different age structures and mortality rates of *Rana luteiventris* between different sites, which were probably due to different microclimate, food availability, and predation rates. Differences in microclimate may also explain differences in age structure between valleys, but I also found that the sexes had different age structures. Microclimate would likely affect both sexes similarly. Therefore, differences in age structure are more likely due to different behavioural patterns of males and females (as discussed below) because sexes share habitats where the microclimate would be the same. Thus, different age structures I found are more likely due to roadkills than due to differences in microclimate.

Further, I did not find a difference between mean age of roadkilled salamanders and mean age of salamanders in RV-R. Age distribution of roadkilled salamanders is like the age distribution of salamanders in RV-R. Thus, there is no tendency that mainly young or mainly old salamanders are killed on the road.

In RV the mean age was lower than in V, but there was a higher site occupancy in RV than in V. Possibly, in V good and large territories may be occupied by old salamanders. Furthermore, in RV younger salamanders may occupy more territories because there are fewer old salamanders which have established their territories. One has to say that in fire salamanders not much is known about territorial behaviour. But different observations say that *Salamandra* species occupy a territory and use it for a long time (*Salamandra salamandra*: Joly 1963, 1968, Himstedt 1994, Catenazzi 1998; *Salamandra lanzai*: Ribéron & Miaud 2000). Furthermore, territorial behaviour is well known from other forest-floor dwelling salamanders, e.g. the red-backed salamanders (*Plethodon cinereus*) (e.g. Mathis 1990, Jaeger 1987/1995, Simons 1997, Townsend & Jaeger 1998). For example, Townsend & Jaeger (1998) found that territorial conflicts over prey are dominated by large males. Thus, possibly such conflicts also occur in fire salamanders and size or age may play a role in territorial defense.

#### **Mean age of males, but not of females, was different between valleys.**

I found that males in RV were younger than males in V and that males in RV-R were younger than males in V. In females, I did not find differences in mean age between valleys or valleysides. Contrary to my expectation, the road effect was stronger on males than on females. I had expected that the road effects would be stronger on females due to the regular breeding migration of females in spring. Thus, males must cross or frequent the road

more often than females for some reasons. Therefore, proportion of males in roadkilled animals should probably be higher than proportion of females. It was impossible to determine the sex of roadkilled salamanders. If males frequent plane structures like roads or forest tracks, there should be more males than females on these structures. Sex of salamanders sitting on the road I did not determine, but I determined sex of some salamanders on forest tracks parallel to the breeding streams where the situation should be similar to the situation on the road. In early May, when females were still migrating to and back from breeding streams, I found a sex ratio of 1:1 on the track. At the end of May, when only few females were still migrating but mating season started, I found a sex ratio of 3.5 males to 1 female on the track. On the webs I found a sex ratio of 2.3 males to 1 female between May and August (Tab. 20).

**Table 20** Sex ratios found on forest tracks and on webs.

Time, place	males	females	sex ratio
early May, forest track	9	9	1:1
end of May, forest track	21	6	3.5:1
May to August, webs	115	49	2.3:1

Thus, it seems that during my study period males were more active than females and that they frequent plane structures actively. Due to different activity levels of males and females during the season, sex ratios of populations can only be determined in long term studies (Thiesmeier 2004). Seifert (1991) found in a nine year study a sex ratio of 1.24 males to 1 female. Rebelo & Leclair (2003) found a sex ratio of 0.96 males to 1 female (6 year study), and Catenazzi found a sex ratio of 0.88 males to 1 females (6 year study). Thus, the strongly male biased sex ratio I found from May to August is probably due to a higher activity of males and not due to a highly male biased population sex ratio. A higher activity of males during my field season would be congruent with a conclusion of Thiesmeier (2004) who states that during mating period males are more mobile than females. Mating season of fire salamanders lasts from May until September. In contrast to a higher activity level of males on forest tracks are my results about distance between recaptures. Recaptured females I found further away from the first capture place than males (Tab. 3). First capture of all of these 5 females has been in the end of May or early June. Thiesmeier (2004) found latest females migrating to the breeding stream in the end of May. Thus, these females were possibly still migrating back from the breeding stream and I therefore found them relatively far away from the first capture place.

But why do males frequent plane structures? Other researchers found that fire salamander males prospect for females (Kästle 1987, Thiesmeier 2004). Possibly they use roads and other plane structures to detect females during the mating period. Since this period is quite

long and males may mate several times, an individual male possibly stays on the road for a long time. Female fire salamanders can store sperm up to two years (Thiesmeier 2004). Thus, females may mate only once during breeding season and not every year and are may therefore be less active than males. If so, females are at a lower risk to get roadkilled than males and therefore the road effect is stronger on males.

### ***Future Prospects***

#### **Road effects on my study population will probably increase in future.**

The road is mainly used by the inhabitants of Ramlinsburg. The number of inhabitants increased over the last years by about 18 humans per year and will probably continue to increase in the future (Tab. 21). Today about 800 cars a day drive on this road. With an increasing number of inhabitants of Ramlinsburg the number of cars on the road will increase and, consequently, also the number of roadkilled fire salamanders. Therefore, the effect of road mortality on abundance and age structure will increase. Ultimately, the viability of the population may decrease.

**Table 21** changes of the number of inhabitants of Ramlinsburg in the last years.

year	nr. of inhabitants	increase
1864	351	
1988	415	64
1998	594	179
2003	693	99

Ramlinsburg



**Figure 12** Study site with village of Ramlinsburg and the road from Ramlinsburg to Lausen.

**Further research should focus on behavioural aspects and on the mechanisms that create the patchy distribution of salamanders within seemingly homogeneous forests.**

Conservation often needs knowledge of behavioural aspects (Sutherland 1998). In fire salamanders, information about migrating behaviour and especially migrating behaviour during the mating season is needed for understanding the effects of roadkills that I found in my study. Do especially males frequent plane structures? Furthermore, territorial defense should be investigated. Does territorial behaviour lead to density dependence, do density dependent regulation mechanisms in fire salamanders exist and can young salamanders establish themselves better if the proportion of old salamanders is low? How does the availability of daily hiding places affect abundance? Understanding the behaviour and habitat use of individuals will help to better understand the impacts of roads on fire salamander populations.

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