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# DIPLOMARBEIT

Titel der Diplomarbeit

„Population size, site fidelity and  
home ranges of male harlequin toads  
(*Atelopus flavescens*) in French Guiana“

verfasst von

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## 1. Introduction

In the last decades a dramatic decline of amphibians all over the world has caught wide attention among scientists and conservationists. Mainly two factors have led to the decrease of amphibian populations: the spread of chytridiomycosis, a fungal disease caused by the pathogen *Batrachochytrium dendrobatidis*, and global warming (Burrowes et al., 2004; Pounds et al., 2006; Rohr et al., 2010). The bufonid genus *Atelopus* has gained particular attention in this context. The genus comprises 102 neotropical species, characterized by small to medium sized, froglike looking, often brightly coloured toads with variable patterns and are therefore also known as the “harlequin frogs” (AmphibiaWeb, August 2013). Many species of this genus suffered from severe decreases in population sizes and some even went already extinct, e.g. *A. ignescens* from Ecuador (La Marca et al., 2005; Ron et al., 2003). Currently, about 80% of the existing species are considered critically endangered (Lötters et al., 2004; IUCN 2012). Populations of many species show an ongoing tendency to decrease thus the status of the whole genus is of great concern. Conservation management for threatened species is needed and therefore in situ conservation activities and ex situ breeding programs have already been established, e.g. the Project Golden Frog for *A. zeteki* in Panama (Zippel, 2002). However, good conservation strategies require profound knowledge on a species’ life history, including its population biology, reproductive strategies, individual behaviour, and demographic characteristics. To acquire this information, surveys and monitoring of populations in their natural habitat are necessary.

Detailed ecological studies have only been conducted for a few members of the genus *Atelopus*, including *A. zeteki* (Lindquist et al., 1996; Karraker et al., 2006) and *A. chririquiensis* (Jaslow, 1974) from Panama, *A. hoogmoedi* from Suriname (Luger et al., 2009), *A. varius* from Costa Rica (Crump, 1986, 1988) and *A. oxyrhynchus* (Dole and Durant, 1974) and *A. cruciger* (Lampo et al., 2011) from Venezuela. Other studies mainly deal with morphological descriptions of (new) species or focus on the phylogeny of the genus and the declines and threats of populations.

Most species of *Atelopus* have distributions which are restricted to a few localities. The degree to which various species are threatened differs but generally lowland species face a lower risk of extinction than species inhabiting higher elevations. In

*Atelopus* we find populations which have undergone declines and are presently severely threatened, while others remain relatively stable and appear to be unaffected (Stuart, 2008; Lips et al. 2003).

Many *Atelopus* species feature a similar lifestyle, e.g. diurnal activity and aggregation of males in proximity to streams, nevertheless there are variations according to reproductive behaviour and breeding phenology (Lötters, 2007). Additionally, differences in site fidelity are also known for this genus. For example, *A. oxyrhynchus* maintains home ranges away from lotic waters during the dry season and returns to its breeding sites along creeks from May to July, during the wet season. There, males occupy perches on logs for up to two months while females usually stay for shorter periods (Dole and Durant, 1974). Males of *A. cruciger* are reported to reside at streams seasonally since they have been encountered at their sites in January, from May to July and in October. Breeding of this species has only been observed in April (Rodriguez et al., 2008, Lötters et al., 2004). Males of *A. zeteki* occupy riverine territories during the whole year, including wet and dry seasons, whereas females reside inside the forest and migrate to streams infrequently (Criswell, 2008). Breeding is assumed to occur during the dry months of November, December and January (Karraker et al., 2006). *Atelopus chiriquiensis* was observed to exhibit high site fidelity along streams during a two-months study in May and June, but it is not clear, whether it maintain long-term territories (Jaslow, 1979). Based on the encounters of amplexant pairs in February, Karraker et al. (2006) presume that oviposition of this species takes place during the dry season. *Atelopus varius* displays behavioural dichotomy: some individuals are extremely sedentary, staying adjacent to streams year-round and defending territories during the wet months, whereas others are roaming around (Crump et al., 1986). From species belonging to the Amazonian-Guianan clade, it is known that *A. franciscus* from French Guiana defends territories near river banks (Boistel et al., 2011). To the best of our knowledge mating of *A. franciscus* was not yet observed, but egg masses and tadpoles were found during the wet months in April and May and it is therefore assumed, that breeding occurs at the onset of the long rainy season (Boistel et al., 2005). Likewise, as reported in a study on *A. hoogmoedi*, the presence of froglets and the absence of females during the wet season indicate, that oviposition takes place already during the somewhat drier period prior to the rainy season (Lötters et al., 2007).

Facing this variability of life strategies, this leads to the need to study other *Atelopus* species in detail in order to gain knowledge on particular species and to assess their status of threat.

The present study investigates aspects of the behavioural ecology of *Atelopus flavescens*, which belongs to the Amazonian-Guianan-clade of the genus (Lötters et al., 2011), such as site fidelity, home range behaviour, and movement patterns. The species is encountered in coastal and central parts of lowland rainforest in French Guiana and little is known about its life history. While males are known to be stream-dwellers, females are rarely encountered near streams and hence it is assumed that they spend most of the time away from lotic water and only migrate to the creeks for reproduction (Lötters, 1996). Mating was not yet observed, but it is assumed that reproduction takes place at the beginning of the rainy season (Gawor et al., 2010).

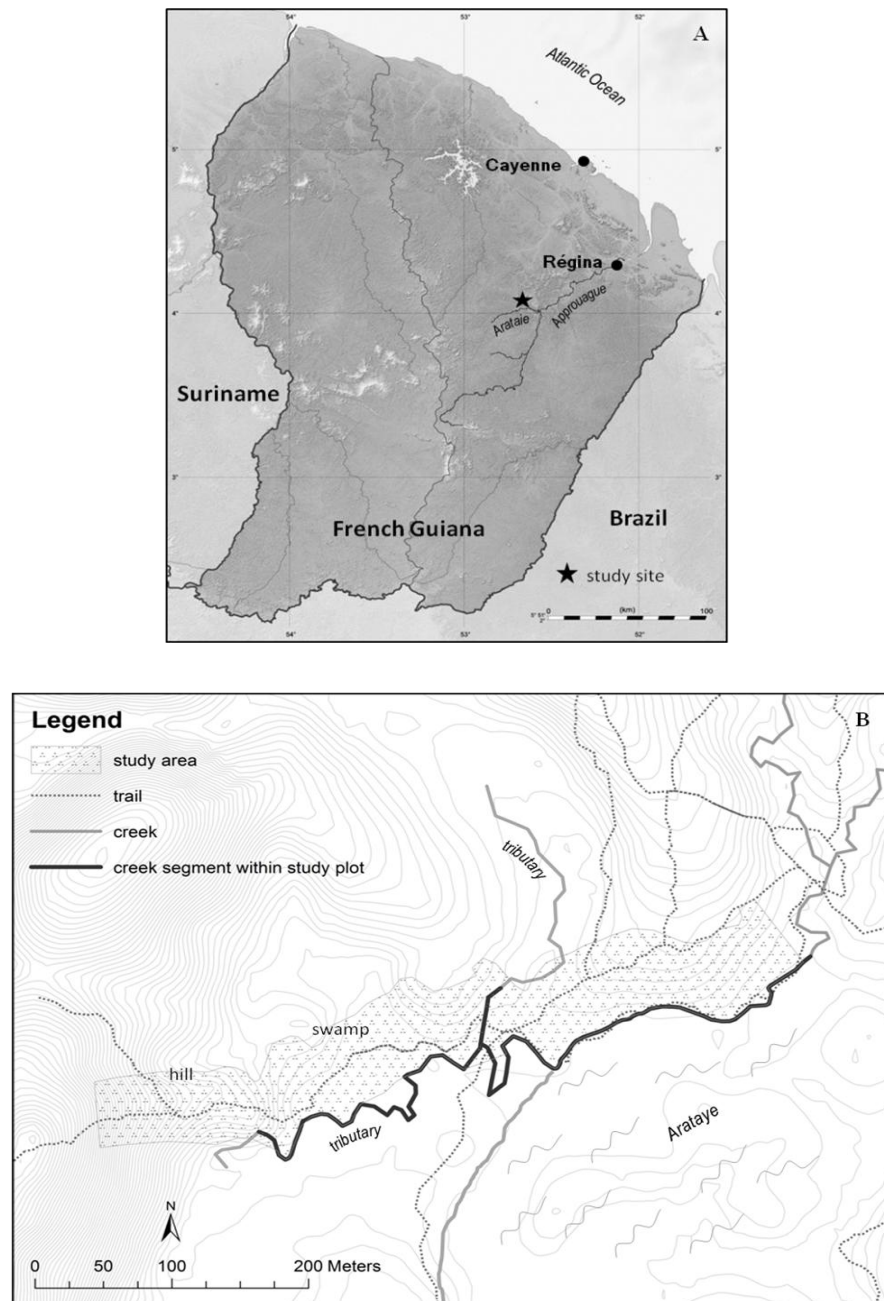
The aim of this study was to gain information on behavioural traits of *A. flavescens* which might be useful to identify susceptibility for possible threats and help to develop ex situ breeding plans for captive populations. As preliminary observations suggest site fidelity in males, it was one of our aims to assure this assumption. Based on the hypothesis that males maintain home ranges for at least a short period of time, activity ranges and movement patterns were determined. Furthermore, the spatial distribution of the population with respect to the habitat was examined and the population size was estimated.

## **2. Material and Methods**

### **2.1. Study area**

The study area is located in tropical lowland rainforest near the field camp “Saut Pararé” (4°02' N - 52°41' W) within the nature reserve “Les Nouragues” in French Guiana (Fig. 1). Field work was conducted along a 1380 m long transect along the river Arataye and two of its tributaries. The study area extended to approximately 3.4 ha at the northern bank of the river and one tributary marking the southern border of the plot. This river segment had the widest streambed and presumably also the greatest depth and flow rate. The creeks within the study area were smaller with streambeds ranging from 1 to 3 m in width and 10 to approximately 100 cm in

depth. Water flow rate in the creeks varied due to vegetation and depth. Stream banks were composed of sand, gravel and plants. Vegetation in the study area is characterized by many small trees and shrubs, while large trees with a stem diameter of more than 50 cm are rare (pers. obs.). Mean annual rainfall at the station varies from 3,000 to 3,250 mm and mean annual temperature is 26 °C (Boyé et al., 1979).



**Figure 1.** (A) Geographical situation of the study area in French Guiana (modified after google maps) (B) Overview of the study plot near the camp Pararé.

## 2.2. Monitoring

Data collection took place from 17 January 2010 to 22 February 2010 and from 30 January 2011 to 25 February 2011, spending 333 and 486 person hours of sampling, respectively. Surveys were conducted daily between 07:00 and 18:00. During this time the entire study plot was searched for individuals from varying starting points so that every part of the study area was surveyed equally and at different times of the day. Furthermore, in the second study period in 2011 night walks were performed on four consecutive nights between 20:30 and 24:00 to check for nocturnal resting sites. Since *A. flavescens* is a diurnal species and hence males are not calling at night at all, only known capture locations were scanned for individuals during the night walks. Toads were located by visual encounter surveys. We tried to locate and capture all individuals which were calling and additionally scanned locations where toads already had been captured before or were assumed to stay. When calling activity was low, previously recorded advertisement calls were broadcast using an mp3-player and loudspeaker to stimulate the males to vocalize. Once captured, the dorsal and ventral patterns of the individuals were photographed with a compact camera (Canon Ixus 10) for individual identification. As reference scale, we used standardized squared paper as photo background thus the size of the toads could be determined later using the public domain NIH Image program (developed at the U.S. National Institutes of Health, USA, and available on the Internet at <http://rsb.info.nih.gov/nih-image/>). Location of first detection, date and time were recorded. Additionally, we noted the following parameters: activity of toads when sighted, substrate where detected and vertical distance from the ground. All parameters were directly recorded in the field using the software ArcPad (ESRI) on GPS-enabled PocketPCs (Ashtech MobileMapper 6). Previously established reference points along the main trail and the creeks within the study area were used for triangulation with precision compasses (Suunto Tandem) to determine the exact position of captured toads. Positions of toads which could not be triangulated were determined by using the GPS function of the PocketPCs.

All geographical data were plotted in ArcMap (ESRI) using a prepared map. Coordinates of capture locations were plotted in ArcMap as point shapefiles. For purposes of easier orientation and better illustration, structures like remarkable trees, logs and rocks were also mapped.



## 2.3. Data analysis

### 2.3.1. Population estimation

For mark-recapture data different methods for estimating the population size exist, depending on the type of population and the according assumptions. Basically, open populations allow for birth, death, immigration and emigration and therefore the count of individuals varies with time. In closed populations we expect none of these parameters to play a role and hence, the total number of individuals within the population remains stable (Williams et al., 2001). The program MARK (White and Burnham, 1999) provides estimation of the population size based on different formulations with variable terms and assumptions. We used the POPAN formulation (Schwarz and Arnason, 1996) in MARK for open populations to estimate the population size for both study periods. It is similar to the Jolly-Seber method with the difference, that animals captured at a specific time are treated as members of a subset of a “super-population”, which are freely moving in and out of the study area (Williams et al., 2001). The assumptions for the POPAN formulation are the same as for the Jolly-Seber method: (1) equal capture probabilities of marked and unmarked animals, (2) equal survival probabilities of animals, (3) no losses of marks and (4) constant size of the study area. Since study animals could be identified uniquely and surveys were conducted regularly through a defined study area, we expect these assumptions not to be violated. We created live encounter histories for each individual, indicating its presence or absence during each survey. Four different models allowing survival ( $\phi$ ) and capture probabilities ( $p$ ) to vary with time ( $t$ ) or being constant over time ( $\cdot$ ) were constructed: (1) a global, fully time-dependent model  $\{p(t), \phi(t)\}$ , (2) a model with constant capture probability and time-dependent survival  $\{p(\cdot), \phi(t)\}$ , (3) a model with constant survival and time-dependent capture probability  $\{p(t), \phi(\cdot)\}$  and (4) a model with constant survival and capture probability  $\{p(\cdot), \phi(\cdot)\}$ . The sin-function was used for capture and survival probabilities, the multinomial-link-function was used for parameter  $p_{ent}$  (probability of entrance) and the log-function was used for super-population  $N$ . We used the goodness-of-fit (*GOF*) test of the integrated RELEASE function in the program MARK for the global model to detect any lack of fit of data and consequently any violation of the assumptions. The extent of overdispersion ( $\hat{c}$ ) which would imply violations of the above-mentioned assumptions, was quantified

as the quotient of  $X^2/df$  (Lebreton et al., 1993). Selection of the best among the four alternative models was based on the Akaike's Information Criterion for small sample sizes ( $AICc$ ) with the lowest value. Population size and standard errors refer to the derived estimates of the best model.

### 2.3.2. Site fidelity and movement

To assess site fidelity, we measured distances between the first capture and the recapture locations in ArcMap for all individuals which were recaptured at least twice. Data from 2010 and 2011 were pooled, since there was no difference in covered distances between the individuals of the two years (Mann-Whitney-U-Test,  $U = 12744$ ,  $p = 0.234$ ). For all individuals we calculated medians rather than means because medians are less sensitive to extreme values reached by rare, large movements made by few individuals.

To analyse movement patterns of *A. flavescens*, the distances between consecutive recapture events were measured for each individual using the analysis toolbox in ArcMap. We calculated median values for each individual and then determined the mean value representing all 98 individuals. To quantify activity in general, we calculated the percentage of observations where individuals had been moving since the last capture event. We categorized observations into "little movement" when distances were less than one meter, "moderate movement" when distances were between one and five meters and "extended movements" which include distances greater than five meters. Furthermore we calculated the biological index of vagility (BIV, Murasaki 2010) for each animal to obtain a comparable parameter for the movement rate. The BIV is calculated as the quotient of the number of movements and captures and leads to a value between 0 (indicating no movement) and 1 (high movement rate). We used distances beyond 25 centimetres as a cut-off for "no movement".

To investigate a possible effect of SUL on movement, we looked for a correlation between SUL and the total distance moved by individuals during the study period as well as median distance moved between recaptures.

For the nine individuals which were captured in 2010 and 2011, the moved year-to-year distance was calculated as the distance between the median centres of each individuals' set of observations points.

All distances were calculated as projected distances in ArcMap.

### 2.3.3. *Home ranges*

We calculated home ranges for individuals with at least five captures using the minimum convex polygon method (MCP, Mohr, 1974). This method creates a convex polygon encompassing all location points of an individual. It is a simple method to estimate home ranges but it comes with the weakness of being sensitive to outliers and hence home range areas are overestimated easily (Seaman et al., 1999, Gautestad and Mysterud, 1993; Sameitz et al., 1997). Nevertheless it is a widely used method and for reasons of comparability we used it in the study. MCPs were calculated in ArcMap using the tool “minimum bounding geometry”. Another commonly used technique to determine home ranges is the kernel density estimation method (KDE, Worton, 1989), which is reported to be more accurate in estimating space use of animals since it is accounting for capture probabilities of an individual. Furthermore, kernel density estimators were shown to be precise with limited data and thus were recommended for use especially in small vertebrates (Murasaki, 2010). Hence, we calculated fixed kernel densities for individuals with at least 10 captures, using the least square cross validation method (LSCV, Rodgers and Carr, 1998, Gitzen et al., 2003) for selecting the smoothing parameter  $h$  (bandwidth). Ranges were calculated for the 50%, 75% and 95% density probabilities using the extension HoRAE toolbox (Steininger and Hunter, 2012) of the software OpenJUMP GIS (Steininger and Bocher, 2009).

To analyse the spatial distribution of individuals with an observed home range we calculated the nearest neighbour distance (NND) as the distance between median centres of each individual’s set of observation points in ArcMap. The median centre is a measure of central tendency of a set of points which is robust to outliers.

### 2.3.4. *Statistics*

We used Microsoft Excel 2010 for data handling and SPSS Statistics 19 for all statistical tests. Kolmogorov-Smirnov-tests were performed to check for normality of parameters. When K-S-tests revealed non-normal distribution of the data, we used Spearman’s correlation coefficient to test for relationship between parameters. Student’s t-test and Mann-Whitney-U-tests were used to check for differences in

parameters of 2010 and 2011 before pooling. Results are presented as means  $\pm$  standard deviation or as medians and their interquartile ranges (IQR). Significance level for p-values was set at 0.05.

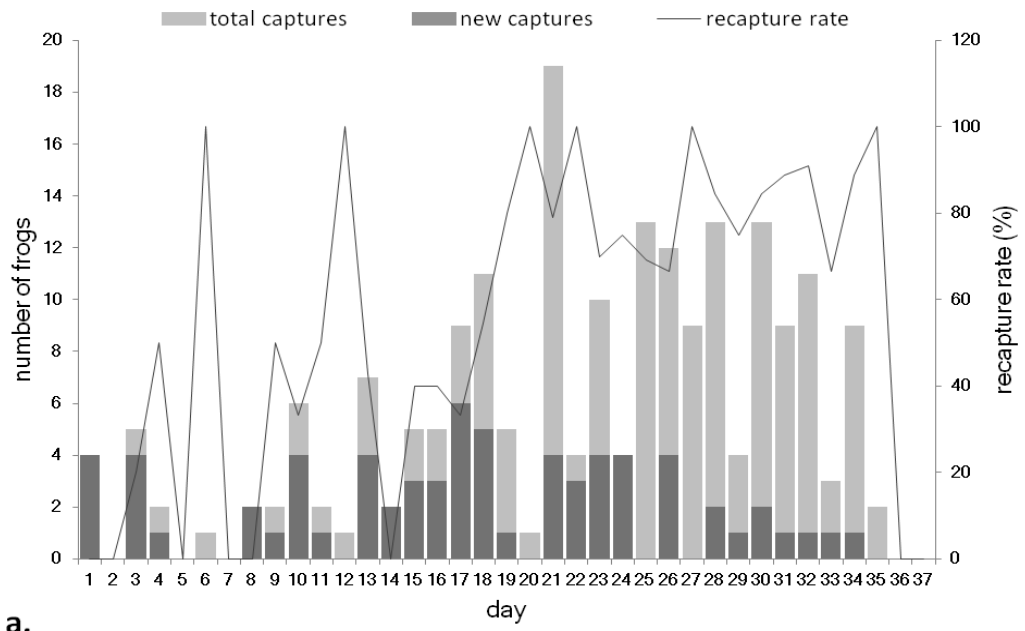
### **3. Results**

#### **3.1. Captures**

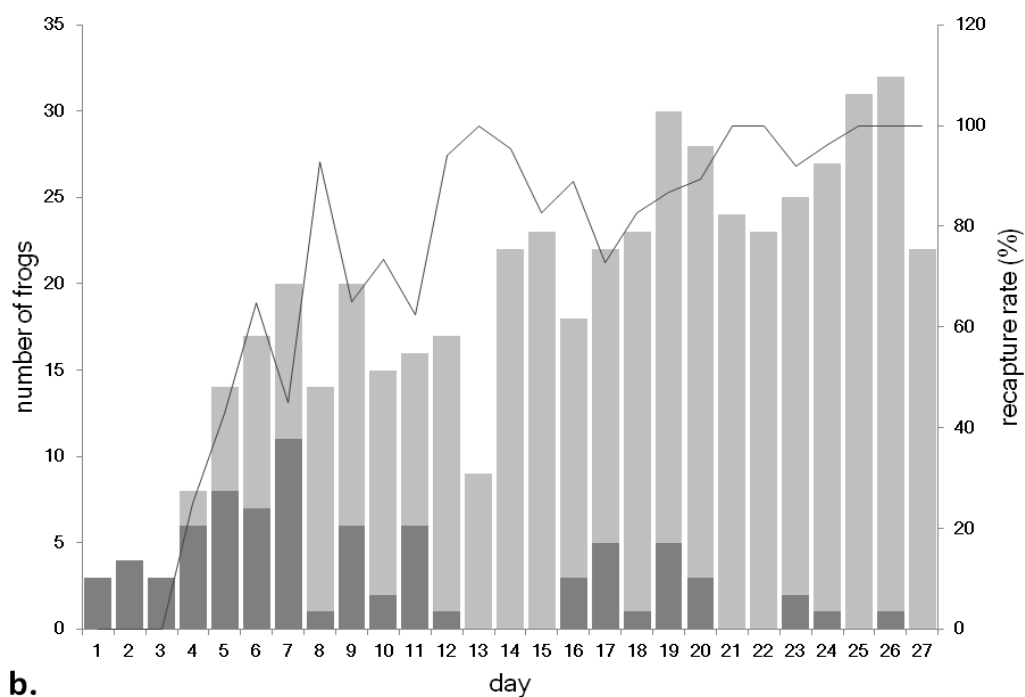
In 2010 66 males were found of which 218 fixes were obtained with a mean recapture interval of 14 (1-33) days. In this study period only one female was found during monitoring within our study area, while 14 females were encountered in the adjacent forest, far from the river and creeks (pers. comm. M. Ringler, W. Hödl, B. Rojas).

Males were located on average three times, ranging from one to 11 captures. 51 of these toads (77%) were captured at least twice, 19 toads (29%) at least five times and only one toad (2%) was found more than 10 times.

In 2011 84 males were found of which 557 fixes were obtained with a mean recapture interval of 15 (1-26) days. During this period the capture rates for individuals were higher than in 2010: males were captured on average six times, ranging from one to 24. 67 males (80%) were located at least twice, 45 males (54%) were found more than five times and 19 males (23%) more than 10 times. No females were found during the study period in 2011.



a.



b.

**Figure 2.** Capture rates during study period in (a) 2010 and (b) 2011. Bars represent captured individuals per day, graphs illustrate daily recapture rate.

### 3.2. Population size

The POPAN model yielded population size estimates of 82 males ( $SE = 6.06$ , 95%  $CI = 70-94$ ) for 2010 and of 93 males ( $SE = 3.62$ , 95%  $CI = 86-100$ ) for 2011. Following the Akaike's Information Criterion ( $AICc$ ) for small sample sizes, the model with time-dependent capture and constant survival probability was the best for each study period (Tab. 1). GOF test results for the global model showed appropriate fit of data for both study periods. TEST 2 of RELEASE, which tests for homogeneous capture probability among individuals was not significant for both study periods (2010:  $X^2 = 27.29$ ,  $df = 37$ ,  $p = 0.89$ ; 2011:  $X^2 = 68.00$ ,  $df = 62$ ,  $p = 0.28$ ) assuring no behavioural response of individuals being captured (Pradel, 1993). TEST 3, which tests for equal survival probability of individuals was also not significant (2010:  $X^2 = 8.13$ ,  $df = 27$ ,  $p = 1.00$ ; 2011:  $X^2 = 37.04$ ,  $df = 32$ ,  $p = 0.25$ ). Corresponding to those results, pooled TEST 2 and TEST 3 support adequate fit of the global model. (2010:  $X^2 = 35.42$ ,  $df = 64$ ,  $p = 1.00$ ; 2011:  $X^2 = 105.04$ ,  $df = 94$ ,  $p = 0.21$ ). The estimation of  $\hat{c}$  indicates that data was not overdispersed and thus the assumptions of independence and homogeneous survival probability of individuals were not violated (2010:  $\hat{c} = 0.54$ ; 2011:  $\hat{c} = 1.12$ ).

**Table 1.** Models constructed with POPAN formulation in program MARK. Models are ranked on the basis of the  $AICc$  value. Models marked with a starlet represent the best models.

Year	Model	$AICc$	$\Delta AICc$	$AICc$ Weights	Model Likelihood	No. of Parameters	Deviance
<b>2010</b>	{p(t), phi(.)}* {p(.), phi(.)}	1027.41 1066.06	0.00 38.65	1.0000 0.0000	1.0000 0.0000	75 39	357.17 491.37
	{p(.), phi(t)}	1111.78	84.06	0.0000	0.0000	74	437.94
	{p(t), phi(t)}	1140.91	113.50	0.0000	0.0000	110	343.21
	<b>2011</b>	{p(t), phi(.)}* {p(.), phi(.)}	1703.54 1723.54	0.00 20.00	1.0000 0.0005	1.0000 0.0001	54 29
	{p(t), phi(t)}	1744.35	40.81	0.0000	0.0000	78	868.14
	{p(.), phi(t)}	1767.53	64.00	0.0000	0.0000	54	943.93

### 3.3. Size and growth rate

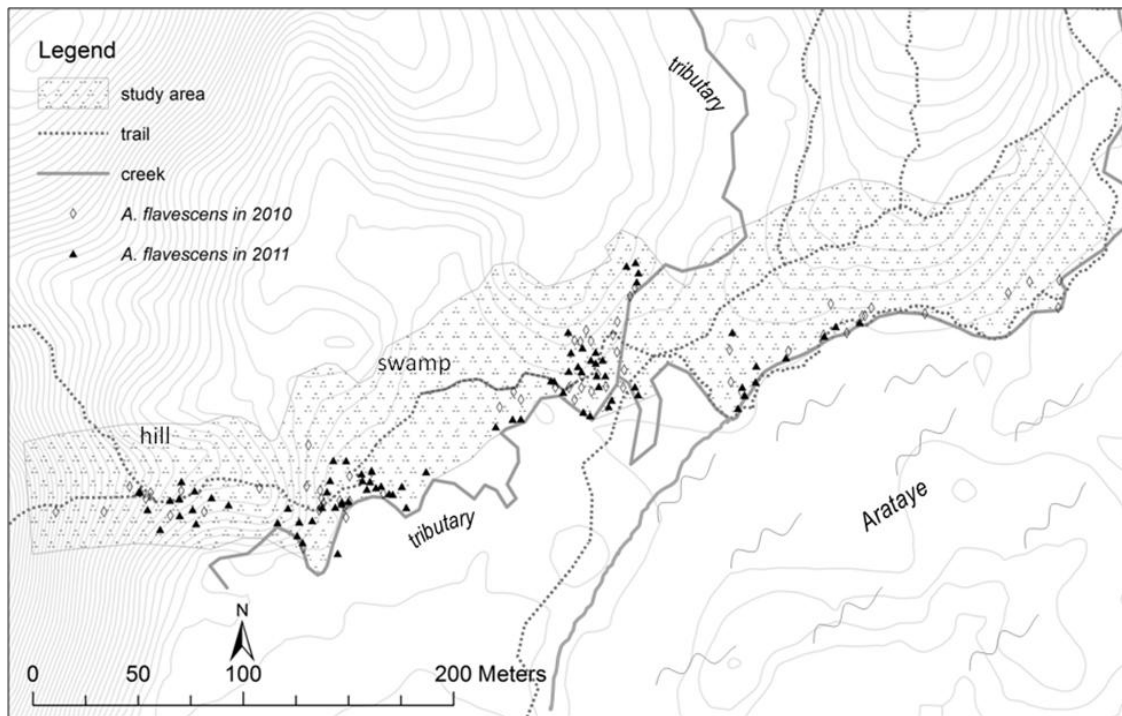
The average snout-urostyl-length (SUL) of captured individuals ( $N = 130$ ) was 24.8 mm  $\pm$  1.5 mm (range = 21.8-28.7 mm). Recaptured individuals from 2010 showed an average growth of 1.3 mm  $\pm$  1.4 mm (range = 0-3.4 mm). Since these values fell

into the reported size range for *A. flavescens* (Rueda et al., 2005) we assumed all individuals to be adult.

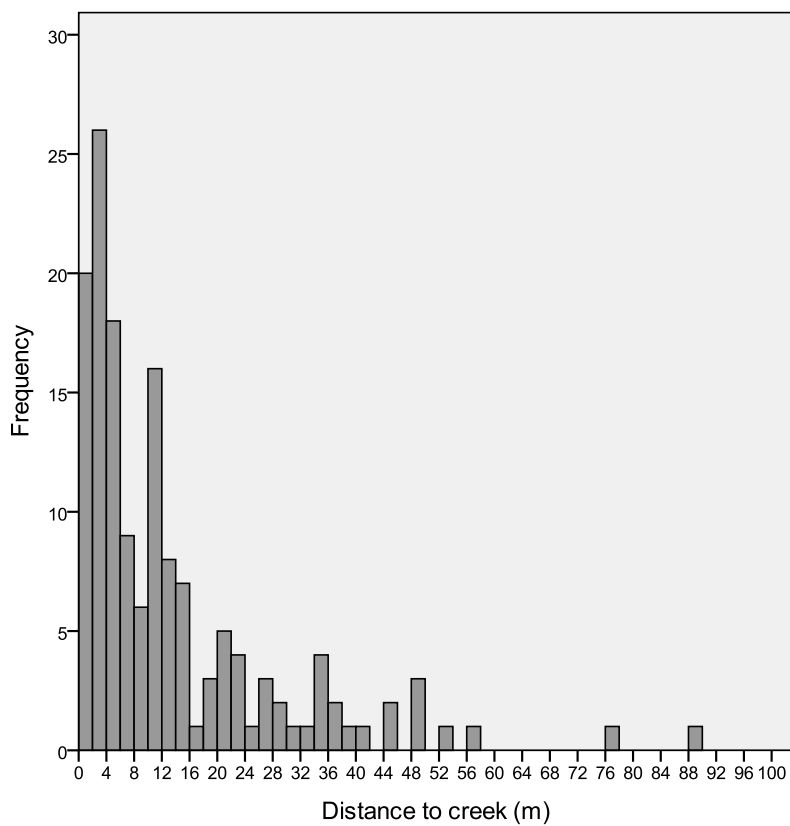
### 3.4. Distribution

Males of *A. flavescens* were not evenly distributed over the study plot. We identified two areas with a high number of individuals, whereas fewer males were found more dispersed in the surrounding area (Fig. 3). In the area between the two “hot spots” not a single individual was found.

The spatial distribution of the individuals within the study plot did not differ much between the two censuses, and only in the easternmost part of the study area, in a small patch along the river Arataye, males were found only in 2010 but not in 2011. Most individuals were located in proximity of the stream. Nearly half of all individuals (41.56%,  $N = 148$ ) were found within a range of 0 to 6 m to the creek (Fig. 4). Median distance to the lotic water was 8.43 m (IQR: 3.24-18.09 m). All distances greater than 19 meters resulted from individuals which were captured on the hill at the edge of the study plot. The furthestmost individual was found 88.96 m away from the creek. Although most parts of the study area cover relatively flat terrain, all distances have to be regarded as lower approximations, since they were calculated as projected distances and not along the slope of the terrain. Hence, actual distances to the creek are larger, in particular for individuals captured on the hill. No correlation was found between the SUL of the males and the distances to the creek ( $r_s = 0.006$ ,  $p = 0.942$ ).



**Figure 3.** Distribution of male *A. flavescens* during both study periods. Rhombuses and triangles represent median centres of each individuals set of observation points.

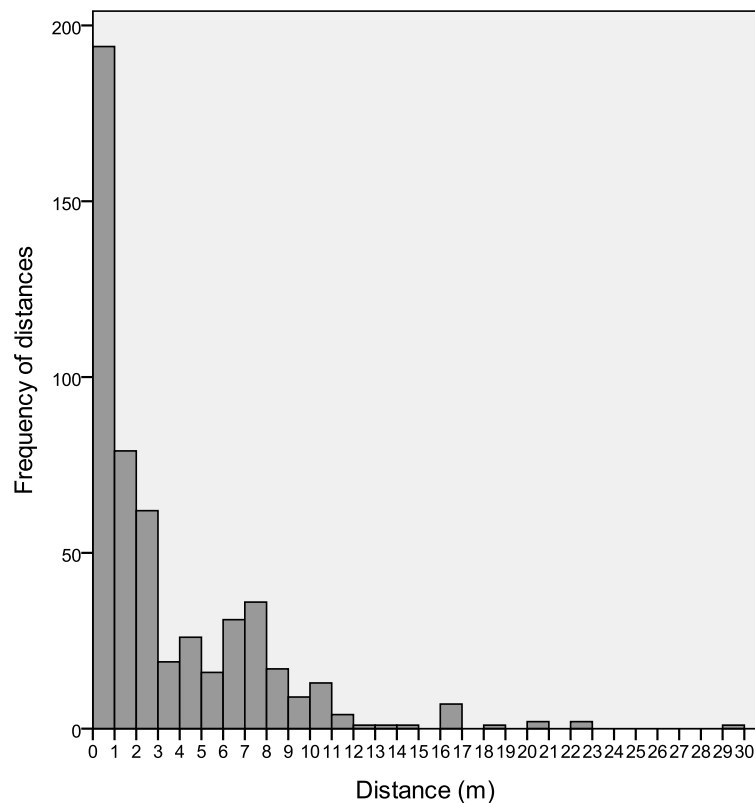


**Figure 4.** Distances ( $N = 148$ ) of individuals to the creek.



### 3.5. Intra-seasonal site fidelity

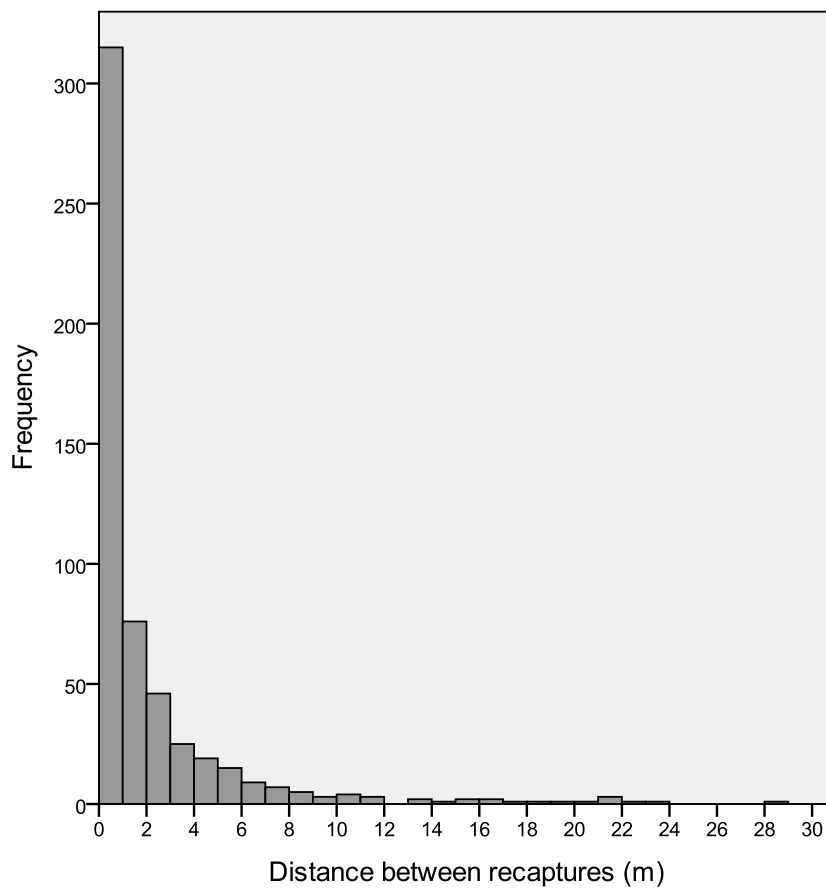
A total of 75 individuals (50% of all captured individuals from 2010 and 2011) were captured at least three times during the study period and were mostly found near their original capture positions. The median distance between the first capture and all respective recapture locations of these males (522 capture events) was 1.8 m (range = 0-29.8 m). Even though several individuals were found quite far from their initial capture location, 37.2% of observations occurred within less than one meter and further 35.6% occurred within less than 5 meters from initial sighting (Fig. 5). Among the nine individuals which were captured in both study periods, four individuals were found within a range to 10 m distant from the capture location of the previous year.



**Figure 5.** Frequency of distances between the first and all subsequent recapture locations of each individual. *N* (522) includes distances from individuals which were recaptured at least twice.

### 3.6. Movement patterns

In 57.9 % (315 out of 544) of all observations the individuals moved distances less than one meter from one capture to the next. In 30.5 % (166) of observations the males were found between one and 5 meters away from their last capture locations and in only 11.6 % (63) of observations males performed extended movements with distances greater than 5 meters (Fig. 6). Many individuals were found repeatedly on the exact same branch or axil of a tree or shrub, others were found on the same plant, but switched their position in the horizontal or vertical axis.



**Figure 6.** Frequency of observations showing distances the individuals moved between capture events ( $N = 544$ ).

Males ( $N = 97$ ) moved a median distance of 1.2 m (IQR = 0.3-2.7 m) between captures, with maximum distances varying strongly among individuals with a range of 0 – 28.6 m (Fig. 6). The mean time span between consecutive captures of the individuals was 14 (1-33) days.

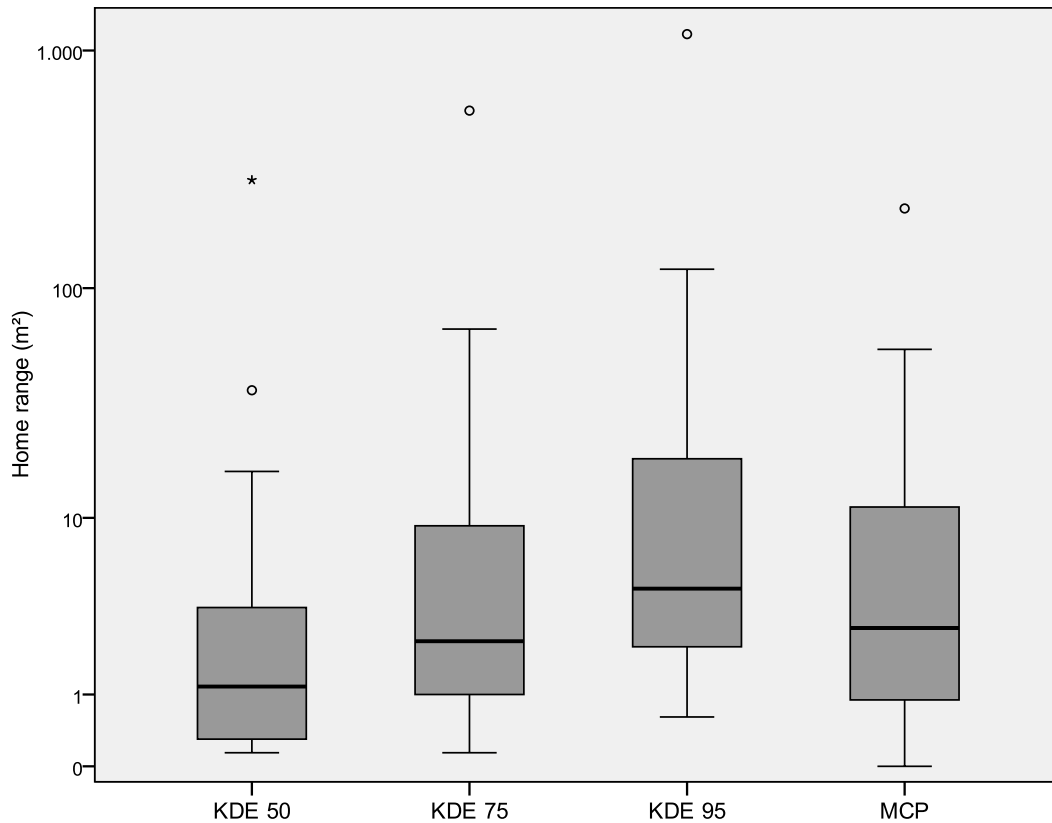
Correlation tests revealed that SUL of males did not affect their movement: there was neither an effect on the total distance moved by the toads during the study period ( $r_s = -0.162$ ,  $p = 0.112$ ), nor on the median distance moved between recapture events ( $r_s = 0.83$ ,  $p = 0.42$ ). The calculation of the biological index of vagility (BIV) revealed high movement rates among 98 individuals with a mean BIV-score of  $0.74 \pm 0.31$ . Only 16 individuals exhibited little movement rate, showing BIV-scores lower than 0.5. The SUL had no effect on the vagility of males ( $r_s = 0.046$ ,  $p = 0.759$ ).

#### *Year-to-year movements*

The nine individuals which were captured in both study periods moved a median distance of 22.80 m (range = 2.89 – 81.15 m) between years. Four of them were found within a range to 10 meters to their capture locations in the previous year. All nine individuals were found within a range of 4.7 m close to the creek in the second study period.

### **3.7. Home ranges**

For 52 individuals MCPs were calculated. Home range sizes were small but differed remarkably among individuals, ranging between 0.0 and 216.90 m<sup>2</sup>. The median home range size was 2.80 m<sup>2</sup> (IQR: 0.88-11.47 m<sup>2</sup>).



**Figure 7.** Box plots representing home range extensions obtained from kernel density and MCP method.

Fixed kernel densities were computed for a total of 17 individuals. Median home range size for the 95% kernel density was 4.56 m<sup>2</sup> (IQR: 2.10-33.52 m<sup>2</sup>), ranging between 0.61 and 1171.53 m<sup>2</sup>. The 75% kernel density resulted in a median home range size of 2.34 m<sup>2</sup> (IQR: 0.86-16.26 m<sup>2</sup>) and the 50% kernel density in a median size of 1.16 m<sup>2</sup> (IQR: 0.29-6.92 m<sup>2</sup>).

Correlations tests revealed, that body size of males did not correlate with home range size (MCP:  $r_s = -0.58$ ,  $p = 0.681$ ; KDE 95%:  $r_s = 1.115$ ,  $p = 0.660$ ).

Despite the great differences in the results of the 95% KDE and the estimates from the MCP method for single males (Appendix I, Tab. 1), no significant difference in home range estimates between the two methods was found (Wilcoxon-test,  $z = -0.781$ ,  $p = 0.435$ ).

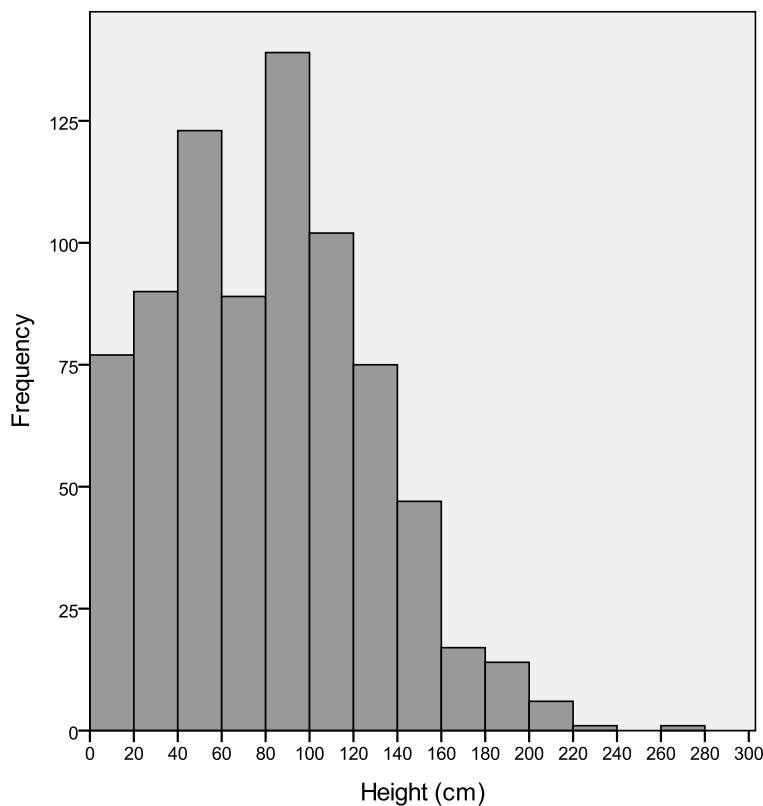
Due to the sparseness of data, no spatial intersections of MCPs were found in 2010. Compared to 2010, MCPs of a total of 18 individuals in 2011 showed overlaps. In

most cases the overlap was related to pairwise intersection of the home ranges, only in one case overlapping of MCPs of four individuals was observed. For the individuals who had overlapping home ranges, the mean percentage of the home range area they shared with neighbours was  $19.99 \pm 23.68\%$ .

The median nearest neighbour distance (NND) for toads with a home range was 4.41 m (IQR: 3.25-7.02 m,  $N = 48$ ). There was no significant correlation between NND and home range size (MCP:  $r_s = -0.013$ ,  $p = 0.933$ ).

### 3.8. Microhabitat and activity

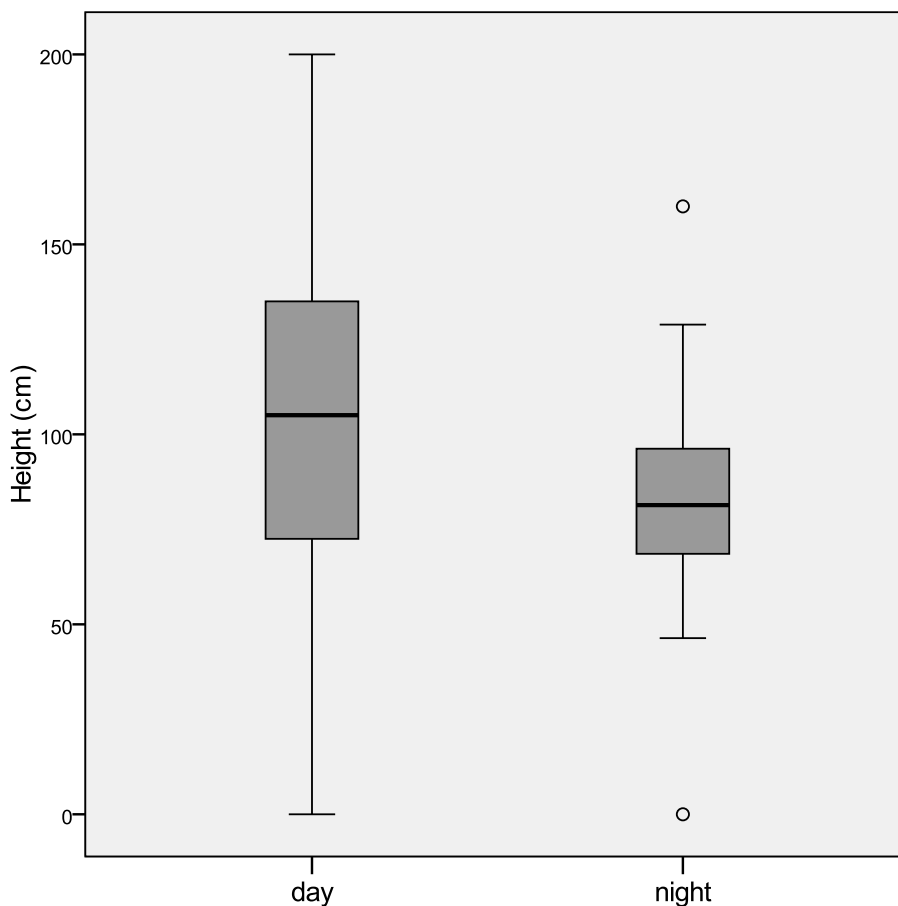
In 64.2 % of the observations male *A. flavescens* were detected on trees and shrubs. Lianas and logs were also used as resting sites (25.9%). Individuals were rarely (9.9%) found in the leaf litter as well as on rocks and only exceptionally on palms. Individuals preferred elevated positions averaging a height of  $78.44 \pm 47.0$  cm ( $N = 781$ ) (Fig. 8). There was no correlation between SUL of males and height ( $r_s = 0.008$ ,  $p = 0.826$ ).



**Figure 8.** Frequencies of height individuals were found.

In 48.27% of observations male *A. flavescens* were detected while sitting and calling, in 45.84% of the observations, individuals were found sitting without vocalizing. Calling activity was highest in the morning and after rainfall. In a few cases, we observed individuals while moving or climbing. We could hardly record any interactions between individuals, only during six observations in 2010 we found males fighting.

During the night we observed males resting mainly on leaves of shrubs and trees. We encountered some individuals ( $N = 23$ ) using the same location as their nocturnal resting site as they used during the day, but the majority of toads could not be detected during nocturnal surveys. Although the difference was not huge, toads moved to less elevated positions for nocturnal resting (T-test,  $t = 3.137$ ,  $p = 0.005$ ) (Fig. 9).



**Figure 9.** Box plot illustrating difference in height from ground between day and night resting sites.

## 4. Discussion

The present study reports first demographic characteristics of *A. flavescens* obtained from a mark-recapture study in the field. Our observations reveal high site fidelity and little home range overlap of adult males, which indicates territoriality in this species. Local distribution of males showed strong association with riverine habitat. Apart from a few exceptions, movements were limited and home ranges were very small.

Females were rarely encountered during our study and except for one, they were found only outside the study area far from the stream, thus corroborating the idea of a spatial segregation of sexes as proposed by Lötters (1996) and McDiarmid (1971). Because of the rare encounters of females during our study period, we do not expect the migration of females to the stream to occur during short dry season and probably not at the onset of the rainy season either. We rather assume that the females arrive at the streams during the wet season. We suspect the rapidly increasing precipitation rate in May in French Guiana (Bongers et al., 2001) to be the trigger for the start of mating in *A. flavescens*. Egg masses of the species found in July (Lescure, 1981) in the region, as well as observations from captive breeding where precipitation was detected to be a strong stimulus for reproduction (Gawor et al., 2012), support our assumptions.

### 4.1. Population size

The obtained estimates of 82 and 93 individuals in 2010 and 2011 only slightly exceed the actual numbers of captured males, indicating that only 19.5% of the population in 2010 and 9.7% of the population in 2011 remained undetected. The high daily recapture rates and the small number of new captures towards the end of the study periods further corroborate that most part of the population had been sampled during our study. A detailed look at the parameter estimates for the survival and capture probabilities from the POPAN model reveals that the capture probabilities of individuals varied temporally and were generally low. The survival probabilities of individuals were very high. Basically, population estimates have a high accuracy when both capture and survival probabilities are high (Wagner et al., 2011). Our results thus suggest intermediate accuracy of our populations. Compared

to the capture probabilities of 2010, the capture probabilities of 2011 were slightly higher. This effect can be linked to the unequal sampling effort since in 2011 two persons conducted surveys instead of one as it was the case in 2010. For future studies on this species, we recommend to increase sampling effort in order to raise detection probabilities to obtain better population estimates.

Although the population size did not decrease from year to year and may seem to be stable, we cannot predict its vulnerability based on our results. Nevertheless, our population estimation can serve as a reference for future studies in this species.

#### **4.2. Distribution**

Our study shows that male *A. flavescens* are strongly associated with riverine habitat and that creek segments in the study area are not equally used. The factors leading to the distribution pattern within the habitat could not be determined from the study. However, the simultaneous occurrence of areas with different densities of individuals might be the result of microhabitat heterogeneity suggesting that sites with optimal habitat characteristics, including good foraging sites, shelter and calling positions are distributed unevenly and therefore males clump at more suitable sites. The absence of males between the two “hot spots” in the study area might be due to the swampier part of the area which is flooded regularly and thus might act as natural barrier. Aggregation of males could also be a response to a female-initiated process where female choice would be facilitated if males occur clumped (Alexander, 1975).

#### **4.3. Site fidelity and home ranges**

Male *A. flavescens* exhibited high site fidelity during our study. Our results show that individuals maintain very small home ranges and movement is mostly restricted to this area. With our data, difficulties occurred in estimating kernel densities from data of individuals who were extremely site faithful and hence capture locations were closely spaced, a problem already recognised by Gitzen et al. (2003). However, overall, both the MCP and the kernel method are acceptable to estimate home range size in *A. flavescens*, but larger sample sizes would improve the results, especially for the kernel density estimates.



The main benefit of site fidelity for *A. flavescens* might be familiarity with the environment and habitat features. Efficient relocation of shelter or optimal calling sites as well as knowing escape routes would increase survival of individuals (Baker, 1978).

During our study we made only few observations of agonistic behaviour in males. In these cases always neighbouring individuals were involved. Besides vocalisations, aggressive displays included kicking, wrestling and crushing the opponent. In order to test the willingness of males to attack intruders, we performed a single preliminary invasion trial where we placed one male into the home range of another male, and as expected, the two males started to fight immediately.

Regarding the facts, that males exhibited high site fidelity, maintained hardly overlapping home ranges and displayed agonistic behaviour, I suggest territoriality in *A. flavescens*, at least in males. The factors leading to this behaviour are not evident from the study. Since our observations fall into the non-breeding season, territoriality appears not to be related directly to mate defence, but still this factor cannot be excluded. Probably, there are several limiting resources, and males establish home ranges long before females arrive. If the ecological resources, which this species needs for survival, are abundant, it is reasonable, that males do not waste time moving around but it would rather be advantageous to be prepared and have territories when females arrive.

#### **4.4. Movements**

Our results show that male *A. flavescens* perform mostly little (up to 1 m) to moderate movements (up to 5 m), but are very vagile since BIV scores were generally very high. These movements can be linked to foraging behaviour, since *Atelopus* belongs to the “ant-specialists” (Toft, 1981) who are actively searching for prey instead of performing a “sit-and-wait” strategy. Apart from the movements within the home ranges, some individuals ( $N = 9$ ) performed single, extended excursions ranging between 10 and 23 m and afterwards returned to their initial location. The reason for the forays is not obvious from our study. Analyses reveal that *A. flavescens* are able to cover large distances in a short period of time. For example, one individual moved 23 m from one day to the next. About half of all individuals ever captured were seen only twice or three times. They covered

distances between 1 and 28 m within time intervals ranging from 1 to 16 days. It is likely, that some of these individuals were not detected often enough to observe them maintaining a home range. Nevertheless, the observations suggest the existence of “sedentary” and “transient” individuals in this population, as it was reported for *A. varius* (Crump, 1986), *A. oxyrhynchus* (Dole and Durant, 1974), and *A. chiriquiensis* (Jaslow, 1979), but further studies are required to confirm this assumption.

Since movements and home range sizes were not related to the body size of males this suggests that larger males do not need to extend their activity ranges to gain enough food because of higher metabolic demands compared to smaller individuals, thus prey availability is probably high at the study site.

Individuals, which were observed in both study periods, moved a mean distance of 22.8 m (range = 2.9 and 81.2 m) from year to year. They either approached the creeks or shifted in lateral direction to the water, but never moved further away. Three individuals migrated 2.9 m, 8.1 m and 31.6 m upstream and one individual moved 32 m downstream. All nine recaptured individuals from the previous year were captured only once or twice in 2010 but were observed to maintain home ranges in 2011. Whether these individuals did not establish home ranges in 2010 or if this behaviour could not be detected – given the smaller sampling effort in 2010 – is not clear. However, immediate proximity to the water seems to be an important and preferable characteristic, since they were all found within a range of 4.7 m from the creek, closer than many other individuals.

#### **4.5. Microhabitat and sleeping position**

Males showed strong preference for shrubs and trees as resting or calling sites, a characteristic which is also seen in *A. hoogmoedi* (Luger et al., 2009). In many toads we observed only little variation in resting positions within the home ranges and the preference of high sites. Elevated positions would be advantageous if used for calling sites but could also serve as optimal perches to facilitate the detection of females. Another benefit could be the conspicuousness of the males themselves: their pink-coloured belly and vocal sac could serve as visual signal in order to attract the females. These assumptions need further investigation for confirmation.

In the present study we report on the characteristics of the resting behaviour in *A. flavescens*. Several individuals used the same locations, e.g. the same shrub or tree where they were found during the day, also as nocturnal resting sites, but most of them moved to less elevated positions. While male *A. flavescens* were observed mainly on branches, axils or stems of shrubs or trees during the day, they changed their nocturnal positions to leaves far from the plants central axis. This behaviour is also seen in *A. zeteki* (Lindquist et al., 2007). While sleeping, perception of animals is generally reduced and thus the risk of being predated increases. Hence, the choice of perching site at night should be considered carefully. The change to nocturnal positions can be addressed to better vigilance via tactile perception of vibrations caused by approaching predators (Lindquist et al., 2007).

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## Appendix I: Results of the home range calculations

**Table 1.** Home range sizes for MCP and 50% (KDE 50), 75% (KDE 75) and 95% (KDE 95) kernel densities.

INDIVIDUAL	KDE 50	KDE 75	KDE 95	MCP
10-m002	3,63	9,19	18,46	54,94
10-m008				1,37
10-m003				0,99
10-m014				0,21
10-m017				0,69
10-m021	1,39	2,82	5,29	0,87
10-m032				1,34
10-m037				3,87
10-m042				0,03
10-m043				1,36
10-m049	0,29	0,14	0,61	0,13
10-m054				3,11
10-m060	0,65	1,44	3,17	2,92
10-m062	0,73	1,70	3,34	17,63
10-m072				0,93
11-m074	285,72	559,34	1171,53	216,90
11-m075				25,86
11-m076				42,49
11-m077				3,06
11-m078				0,14
11-m079				1,73
11-m082				10,74
11-m083				3,82
11-m084	0,30	1,10	2,61	43,94
11-m085				13,36
11-m087				0,16
11-m090	2,08	4,95	11,28	9,85
11-m091				12,71
11-m092	36,70	67,05	120,25	15,26
11-m094	0,46	1,00	2,17	2,97
11-m095				0,86
11-m096	0,17	0,32	0,93	6,14
11-m097	10,20	23,33	48,58	11,71
11-m098	16,22	29,55	49,13	7,13
11-m100	1,18	2,90	7,11	5,23
11-m101	0,14	0,29	0,69	1,24
11-m105	1,16	2,34	4,56	1,07
11-m106				18,82
11-m107				36,11
11-m108	0,28	0,70	2,03	3,51
11-m110				0,22
11-m111				2,45
11-m113				2,49
11-m114				0,43
11-m115				1,96
11-m117				35,28
11-m120				4,28
11-m121				2,67
11-m123				1,15
11-m126				0,02
11-m129				19,93
11-m134				0,22
11-m137				2,26
11-m149				0,39

## Appendix II: Encounter history files

### Encounter history file of 2010

/*m002*/	1000000001000000000000000000000000	1;
/*m003*/	1000000000011000110010011000001011000	1;
/*m004*/	101001000010000000001010000100000000	1;
/*m005*/	0011000000000010001000000100010101000	1;
/*m006*/	0010000000000000000000000000000000	1;
/*m007*/	0001000000000000100000000000000000	1;
/*m008*/	0010000000000000000000000000000000	1;
/*m009*/	0010000001000000000000000000000000	1;
/*m010*/	000000011000000000000100000000000000	1;
/*m011*/	0000000100000000000000000000000000	1;
/*m012*/	0000000010000000000000000000000000	1;
/*m014*/	000000001001000010000100001010000000	1;
/*m015*/	0000000001000000000000000000000000	1;
/*m016*/	000000000100100000000100000000000000	1;
/*m017*/	000000000100000010001110000000000000	1;
/*m018*/	0000000000100000000000000000000000	1;
/*m019*/	000000000000100000000000110100000000	1;
/*m020*/	0000000000001000000010101000000100000	1;
/*m021*/	0000000000001010000000000000000000	1;
/*m022*/	0000000000001000000000000000000000	1;
/*m025*/	0000000000001000000000000000000000	1;
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## Appendix III: Abstract/ Zusammenfassung

### Abstract

Toads of the bufonid genus *Atelopus* are found through a wide range of neotropical regions. Linked to the global spread of chytridiomycosis and global warming, many species of this genus suffered from dramatic population declines in recent years while others remained unaffected. To develop conservation strategies, data on behavioural and ecological traits as well as on demographic parameters are needed, but still lacking for many species.

The present study is the first to provide information on the population size, site fidelity and home range behaviour of *Atelopus flavescens* obtained from a population in French Guiana. In two consecutive years, we conducted a capture-mark-recapture study to estimate the population size and to assess site fidelity and movement of the toads. Home ranges of males were calculated using the minimum convex polygon method and kernel density estimation. Furthermore, the local distribution of toads and resting behaviour is reported.

During our study we only observed males, hence we do not expect the migration of the females to streams to occur during the “short dry season” in February, March and April, which interrupts the rainy season in French Guiana and is characterised by low daily precipitation of 1 to 10 mm (Bongers et al., 2001). Population size estimation for the sampled locality in Nouragues resulted in 82 individuals for 2010 (20 individuals/ha) and 93 individuals for 2011 (30 individuals/m<sup>2</sup>) within the study area of 3.4 ha. Recruitment during our study period was low, suggesting that male *A. flavescens* establish their home ranges long time prior to the arrival of females. Male toads aggregated along streams, but their distribution within the study area was not uniform.

Males exhibited high site fidelity for the duration of our study periods, but not between years. Nine individuals found in 2010 were recaptured in the following year. These individuals moved a median distance of 22.8 m and maintained home ranges in the second census. Proximity to the water seems to be an important factor, since all nine recaptured toads were found within a range of 4.7 m close to the stream. Given the fact, that 50% of all sampled individuals from both study periods exhibited high site fidelity being captured at least three times near their original

detection site, while the remaining were captured once or twice but never recaptured, the existence of “sedentary” and “transient” individuals is suggested for this species, corroborating findings in other *Atelopus* species.

Generally, males maintained very small home ranges: median size was 2.80 m<sup>2</sup> calculated with the MCP method and 4.56 m<sup>2</sup> using the 95% kernel density estimator. Home ranges hardly overlapped, indicating territoriality of males, at least during the non-breeding season. The biological index of vigility revealed a high movement rate of the toads, but their movements were restricted to small areas. Some individuals performed occasionally forays up to 28.6 m and returned to their original site. Males showed a strong preference for shrubs and small trees as resting sites and preferred elevated positions, which might improve their ability to detect females. During the night, most of the toads could not be found at their calling sites. Those detected were found on leaves at lower heights.

Our study reveals behavioural characteristics such as site fidelity, movements and habitat association of male *A. flavescens*. However, further long-term studies on this species are required to gain information on other important life history traits such as reproduction, which still remains an unsolved mystery in *A. flavescens*.

## Zusammenfassung

Die artenreiche Gattung der Stummefußkröten (*Atelopus*) ist innerhalb der Neotropen weit verbreitet. Aufgrund einer mittlerweile weltweit auftretenden Pilzkrankheit, der Chytridiomykose, und des Klimawandels erlitten viele Arten dieser Gattung in den letzten Jahren einen starken Populationsrückgang, während andere jedoch davon unberührt scheinen und stabile Populationen aufweisen. Fundierte Managementpläne für gefährdete Organismen erfordern ein grundlegendes Wissen über die Eigenschaften und damit die Bedürfnisse der jeweiligen Art, welches jedoch für viele *Atelopus*-Arten fehlt.

Die vorliegende Studie ermittelt erstmals Informationen über verhaltensökologische Merkmale von *Atelopus flavescens*, der Gelben Stummelfußkröte, welche im Zuge einer Freilandstudie in Französisch Guyana beobachtet wurden. Über einen Zeitraum von jeweils einem Monat in zwei aufeinanderfolgenden Jahren führten wir eine Fang-Wiederfang-Studie durch, um die Populationsgröße abzuschätzen sowie die Standorttreue und Wanderbewegungen der Kröten zu ermitteln. Aus den Daten berechneten wir mithilfe der Minimal-Konvexen-Polygon-Methode (MCP) und der Kerndichteschätzung (KDE, kernel-density-estimation) die Größe der Aktionsradien der Männchen und analysierten die räumliche Verteilung der Kröten innerhalb des Untersuchungsraums. Weiters gibt unsere Studie Einblick in die nächtlichen Ruheplätze von *A. flavescens*.

In unserem Untersuchungsgebiet entlang mehrerer kleiner Bäche fanden wir fast ausschließlich männliche Tiere. Weibchen wurden - bis auf eine einzige Ausnahme - außerhalb des Untersuchungsgebiets fern von Fließgewässern angetroffen. Während unserer Untersuchungsperiode in der sogenannten „kurzen Trockenzeit“, welche von Februar bis April andauert und niedrigen täglichen Niederschlag (zwischen 1 und 10 mm) aufweist (Bongers et al., 2001) konnten wir keine Wanderung der Weibchen zu den von zahlreichen, rufenden Männchen benutzten Standorten feststellen.

Die von uns untersuchte Population in Nouragues wurde auf 82 Individuen für 2010 (0.002 Individuen/m<sup>2</sup>) und 93 Individuen für 2011 (0.003 Individuen/m<sup>2</sup>) auf einer Fläche von 3.4 ha geschätzt. Generell aggregierten sich die Männchen in der Nähe von Bächen, jedoch ergab unsere Untersuchung, dass die räumliche Verteilung nicht gleichförmig war. Vielmehr fanden sich Individuen in Arealen mit höherer

Individuendichte („hot spots“) zusammen. Die Männchen zeigten eine ausgeprägte Standortstreue innerhalb der beiden Beobachtungszeiträume (2010: 37 Tage, 2011: 27 Tage) jedoch nicht von Jahr zu Jahr. Neun Individuen, welche wir 2010 beobachtet hatten, wurden im darauffolgenden Jahr wiedergefangen. Diese wanderten im Schnitt eine Distanz von 22.8 m und behielten ihre „home ranges“ während der gesamten zweiten Beobachtungsperiode. Unmittelbare Nähe zum Bach schien dabei ein wichtiges Kriterium für den Standort zu sein, da diese neun Wiederfänge alle in einer Entfernung von bis zu 4.7 m vom Bach entfernt gefunden wurden. Aufgrund der Tatsache, dass 50% der Individuen sehr standorttreu waren und mindestens dreimal während des Untersuchungszeitraumes gefangen wurden, während die restlichen nur ein oder zweimal gesichtet wurden, vermuten wir bei dieser Art das gleichzeitige Vorkommen von sesshaften, standortstreuen und sich in diesem Gebiet nur temporär aufhaltender Tiere, welche sich womöglich auf Durchzug befinden.

Wir stellten fest, dass die Männchen sehr kleine Aktionsradien besitzen: Berechnungen mit der MCP-Methode ergaben eine durchschnittliche Größe von 2.80 m<sup>2</sup>, jene mittels KDE-Methode 4.56 m<sup>2</sup>. Die Aufenthaltsräume überschneiden sich nur minimal, was auf territoriales Verhalten der Männchen hinweist, zumindest außerhalb der Paarungszeit. Die Tiere zeigten eine hohe Bewegungsrate, allerdings auf nur sehr kleinem Raum. Unter den standortstreuen Tieren beobachteten wir einige Individuen, welche auch einzelne, weitere Strecken zurücklegten, jedoch anschließend wieder in ihren „home range“ zurückkehrten.

Die Individuen hielten sich bevorzugt auf erhöhten Plätzen in Sträuchern und kleinen Bäumen auf, was ihnen vermutlich erleichtert, ankommende Weibchen und konkurrierende Männchen zu entdecken.

Jene Individuen, die wir nachts aufspürten, wurden auf Blättern ruhend gefunden, meist in geringerer Höhe als tagsüber.

Mithilfe unserer Studie konnten Erkenntnisse über verhaltensökologische Aspekte wie Standortstreue, Aktionsradien und Wanderbewegungen in Zusammenhang mit dem Habitat der Kröten gewonnen werden. Um Informationen über weitere wichtige Ereignisse der „life history“ wie z.B. die Fortpflanzung und die völlig ungeklärten Aktivitäten der Weibchen zu gewinnen, bedarf es jedoch weiterer Untersuchungen.

## Appendix IV: Curriculum vitae

Name Tanja Himmel  
Geburtsdatum 12.01.1987  
Geburtsort Wien  
Staatsbürgerschaft Österreich  
Familienstand ledig  
Adresse Steinhagegasse 4/10, 1120 Wien

### *Studienverlauf*

Seit 10/2008 Diplomstudium Veterinärmedizin, Vetmed Wien, 3. Abschnitt  
Seit 11/2007 Studium Zoologie, Universität Wien  
10/2005 - 11/2007 Studium Biologie mit Erhalt des 1. Diplomzeugnisses, Universität Wien

### *Berufserfahrung*

Seit 01/2008 geringfügig Angestellte als Mitarbeiterin der Zoopädagogischen  
Abteilung, Tiergarten Schönbrunn Ges.m.b.H.

### *Besondere Auszeichnungen*

01/2011 Leistungsstipendium der Uni Wien für das Studienjahr WS 08/SS 09  
01/2010 Leistungsstipendium der Uni Wien für das Studienjahr WS 09/SS 10

### *Auslandsaufenthalte zu Studienzwecken und Fortbildungen*

09/2013 '9<sup>th</sup> International Conference on Behaviour, Physiology and Genetics of  
Wildlife', Leibniz Institut für Zoo- und Wildtierforschung, Berlin  
07/2013 Summer School 'Exotic Medicine and Surgery', University of Veterinary  
and Pharmaceutical Sciences Brno, Tschechien  
05/2013 'International Conference on Diseases of Wild and Zoo Animals', Vienna  
05/2012 '2<sup>nd</sup> International Conference on Reptile and Amphibian Medicine',  
Cremona, Italien  
02/2011 Französisch Guyana, Feldarbeit im Rahmen der Diplomarbeit für  
Zoologie  
02/2010 Projektpraktikum „Ethoökologie und Diversität neotropischer  
Amphibien“, Französisch Guyana  
08 - 09/2010 Volontariat „Sea Turtle Course“, einem Artenschutzprogramm für die  
Unechte Karettschildkröte (*Caretta caretta*) in Fethiye, Türkei

### *Weitere Qualifikationen*

Sprachen Englisch in Wort und Schrift  
Grundkenntnisse in Spanisch, Französisch, Italienisch  
Computerprogramme Word, Powerpoint, Excel, ArcGIS, SPSS, MARK, Photoshop