



Male life history of a harlequin toad population in French Guiana

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Abstract. Harlequin toads (*Atelopus* spp.) constitute one of the most threatened amphibian clades worldwide, yet much of their life history remains poorly understood. These anurans are strongly associated with stream environments, which are used for reproduction and occupied by males throughout the year, while only visited by females during the reproduction season. We studied a population of the *Atelopus flavescens* complex in French Guiana. We describe male population density, habitat use, site fidelity and movement, as well as home range behaviour – all prior to the arrival of females. We also present further natural history observations such as nocturnal resting sites and anecdotal observations of females. Our findings suggest that in this lowland population of *Atelopus*, males maintain territories for a relatively long time compared to other species. Within them, they acoustically compete for females, which they attempt to clasp for amplexus when they arrive later in the season on their way to the breeding sites.

Key words. Amphibia, Anura, Bufonidae, *Atelopus*, spatial habitat exploitation, home range, lowland, movement, population density, site fidelity.

Introduction

The genus *Atelopus*, known as harlequin toads, comprises small, mostly diurnal, and often colourful anurans that are associated with stream environments in the Panamanian and Neotropical realms (sensu HOLT et al. 2013). In this monophyletic group, more than 100 species are recognized (not all formally described), most of which live in montane habitats, but several taxa also occur in lowland regions (LA MARCA et al. 2005, LÖTTERS et al. 2011). In the lowlands of the eastern Guiana shield, *Atelopus* comprises a group of closely related forms. They are referred to as the Guianan clade, which is nested within the Amazonian-Guianan clade (LÖTTERS et al. 2011). In this group, six

species or subspecies have been described, but the validity of most is part of an ongoing debate. Species boundaries remain ambiguous because of overall similar adult and larval morphology, while at the same time coloration varies markedly among populations (LESCURE 1981, BOISTEL et al. 2005a, LÖTTERS et al. 2022). Using molecular genetics, at least two main groups can be distinguished within the Guianan clade; one is the *A. flavescens* complex (comprising the nominal taxa *A. flavescens*, *A. franciscus*, *A. spumarius barbotini*, *A. vermiculatus*), while the other includes the *A. hoogmoedi* complex (NOONAN & GAUCHER 2005, S. LÖTTERS unpubl. data).

Given that harlequin toads are among the most threatened amphibians worldwide, with currently more than

two thirds of the described species categorized as ‘Critically Endangered’ (IUCN 2021) and many of them likely to be extinct (LA MARCA et al. 2005, RUEDA-ALMONACID et al. 2005), it is particularly important to better understand their biology. Only when species are comprehensively understood, we are able to suit effective in situ and ex situ conservation measures (cf. LÖTTERS 2007, GAWOR et al. 2012).

This need stands in sharp contrast to the poor knowledge on *Atelopus* life history. Most of the available information is anecdotal, e.g. sporadic observations added to species descriptions, and only few taxa have been in the focus of systematic ecological and behavioural studies (SEXTON 1958, DOLE & DURANT 1974, JASLOW 1979, CRUMP 1983, 1986, 1988, LINDQUIST & HETHERINGTON 1996, LÖTTERS 1996, KARRAKER et al. 2006, LINDQUIST et al. 2007, LAMPO et al. 2012, ROCHA USUGA et al. 2017, RUEDA-SOLANO et al. 2022). Among the harlequin toads of the Guianan clade, only the life history of *A. hoogmoedi* has been studied (LUGER et al. 2009, NICOLAÏ et al. 2017) in the Brownsberg Nature Park in Suriname (DE DIJN et al. 2007) and in the Iwokrama Forest Reserve in Guyana (HAWKES & WALL 1993).

In this study, we investigated life history aspects of a population of the *A. flavescens* complex in French Guiana. Like in all harlequin toads, reproduction in this population takes place in small streams. Males show a strong association with stream environments throughout the year, while females are found near water only for reproduction, which takes place from April to May (BOISTEL et al. 2005a). The purpose of this study was to describe male population density, spatial habitat exploitation, site fidelity, and movement, as well as home range behaviour – all prior to the arrival of females.

Methods

Study species

The taxonomic status of the *Atelopus* population at our study site is currently disputed. NOONAN & GAUCHER (2005) studied phylogeographic aspects of French Guianan *Atelopus* and found that the population at our study site is genetically similar to other populations identified as *A. franciscus* LESCURE, 1973. Likewise, in a study on hearing abilities in *Atelopus*, BOISTEL et al. (2011) applied this name to a nearby population. However, the status of *A. franciscus* as a valid taxon has been doubted, as it is genetically similar to populations allocated to *A. flavescens* DUMÉRIL & BIBRON, 1841 (NOONAN & GAUCHER 2005) and because of shared morphology of larvae from populations of both *A. flavescens* and *A. franciscus* (BOISTEL et al. 2005a). Moreover, while *A. franciscus* was originally discriminated from *A. flavescens* on the basis of darker colouration and smaller size (LESCURE 1973), subsequent studies have demonstrated a generally greater variability in these traits among Guianan harlequin toads (BOISTEL et al. 2005b, NOONAN & GAUCHER 2005). This indicates that the two proposed species might be conspecific, with the older name *A. flavescens* having priority. Therefore, in the absence of a comprehensive taxonomic revision, we here refer only to the *A. flavescens* complex.

In the population studied by us (locality details below), adult males have a snout-urostyle length (SUL) of 24.8 ± 1.5 mm (range = 21.8–28.7 mm, N = 136). Dorsal colours and patterns are highly variable, as demonstrated in Figure 1; ventral surfaces are pink. We determined sex and maturity via the presence of calling behaviour and nuptial



Figure 1. Dorsal pattern variation in the population of the *Atelopus flavescens* complex at the study site ‘Saut Pararé’. Top left image shows a female, all other images show males. Photos: PHILINE WERNER.

pads. The species is diurnal, like most members of the genus *Atelopus* (SEXTON 1958, DOLE & DURANT 1974, CRUMP 1983, 1986, 1988, LINDQUIST & HETHERINGTON 1996, LÖTTERS 1996, KARRAKER et al. 2006).

Field data collection

We conducted fieldwork in tropical lowland rainforest (Fig. 2) near the camp 'Saut Pararé' of the CNRS Nouragues Ecological Research Station (4°02' N, 52°41' W, 30 m a.s.l.) within the nature reserve 'Les Nouragues', French Guiana (BONGERS et al. 2001) (Fig. 3b). Mean annual rainfall at the station varies from 3,000 to 3,250 mm and mean annual temperature is 26° C (BOYLE et al. 1979). We conducted population surveys along a 1,380 m long trail, which followed the left bank of the river Arataye and continued upstream along a tributary creek. From the banks, the study plot extended northwards, covering an area of 4 ha (Fig. 3a). Along the river segment of our study plot, the Arataye has a maximal width of ~250 m and features several small islands and sections with rapids, resulting in flow channel widths of 5–40 m. Here, water depth typically is 0.5–2 m, which can increase considerably after strong rainfalls. The creeks within the study plot are smaller with streambeds ranging from 1–3 m in width and 10–100 cm in depth. Water flow speed in the creeks varies due to vegetation and depth. Stream banks are composed of sand, gravel and plants. Many small trees and shrubs characterise the vegetation in the area next to the creeks, while large trees with a stem diameter of more than 50 cm occur only in the area associated with the river. During the rainy season, the creeks regularly experience backwater from the river, causing complete flooding of the neighbouring area for up to several days.

We monitored the population from 17 January to 22 February 2010 (PW, ML) and from 30 January to 25 February 2011 (TH plus one to three field assistants), during the short rainy season in French Guiana, spending 333 and 486 person hours in the field, respectively. We conducted



Figure 2. Typical vegetation in our study plot in the Nouragues Reserve. Photo: MAX RINGLER.

visual encounter surveys (HEYER et al. 1994) daily between 07:30 and 18:00 h, matching the activity period of the studied harlequin toads. During this time, we opportunistically searched the entire study plot for individuals, starting from varying points to achieve an equal spatial and temporal sampling coverage across the area. In addition, during the 2011 study period, we performed nocturnal surveys on four consecutive nights (22–24 February 2011) between 20:30 and 24:00 h to ascertain suspected nocturnal resting sites of males at known diurnal capture locations.

We tried to locate and capture all calling individuals (i.e., males) and additionally carefully examined locations where toads had been captured previously. When calling activity was low, we performed playbacks of advertisement calls using a digital music player (G-Flash 512; Maxfield, Düsseldorf, Germany; company discontinued) and a battery powered loudspeaker (SRS-M30; Sony, Tokyo, Japan) to stimulate *Atelopus* males to vocalise. Once caught, we photographed the toads' dorsal and ventral patterns with a digital camera (Ixus 10; Canon, Tokyo, Japan) for individual recognition. As a reference, we used paper with a 5-mm grid as a photo background and later determined toad SUL from the dorsal images with the software Image J (RASBAND 1997–2021).

We recorded all captures with date and time, encounter substrate, height above the ground, and any behavioural observations on a digital map (RINGLER et al. 2016) using the portable GIS software ArcPad 8.0 (ESRI, Redlands, CA, USA) on GPS-enabled PocketPCs (MobileMapper 6; Ashtech/SpectraPrecision, Westminster, CO, USA). We used reference points along an existing trail and in the creeks to triangulate the toad positions with precision compasses (Tandem; Suunto, Vantaa, Finland), using the '2-point offset' function in ArcPad. For locations with no direct line of sight to the reference points, we used the GPS function of the MobileMappers. We used ArcMap 10.6 (ESRI) to manage, analyse, and plot spatial data.

Due to a failure of the mapping device, in 2010 we temporarily had to flag capture locations for later mapping with a replacement device. During this time, we only recorded toad identity and location descriptions together with capture date and time. Before we could resume mapping, the study plot got inundated after several days of heavy rainfall. As a result, several location markers were lost or became inaccessible until the end of our stay. Therefore, not all captures from 2010 have the accompanying spatial information. The resulting sample sizes, which diverge for spatial and mark-recapture analyses, are given in the results.

Data analysis

We performed Kolmogorov-Smirnov tests to test for normality of parameters. With non-normal distributions, we used Spearman's correlation coefficient to test for relationship between parameters. We used Student's t-tests and Mann-Whitney U tests to examine differences in parame-

ters of the 2010 and 2011 datasets before pooling. Results are presented as median ranges. Significance level for p-values was set at 0.05. For data handling we used MS-Excel (Microsoft, Redmond, WA, USA) and we conducted all statistical tests in PAST 4.06b (HAMMER et al. 2001, HAMMER 2021).

Male Population size. We used the 'POPAN' formulation of SCHWARZ & ARNASON, (1996) implemented in the software MARK (WHITE & BURNHAM 1999) to estimate the total population size for both study periods. POPAN is specifically intended for the use with demographically open populations and has been successfully applied to anurans (e.g. WAGNER et al. 2011). 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 plot (WILLIAMS et al. 2002). 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 plot. Since we could unequivocally identify individual toads and aimed at an equal spatial and temporal sampling throughout the defined study plot, we assume that these assumptions were not violated.

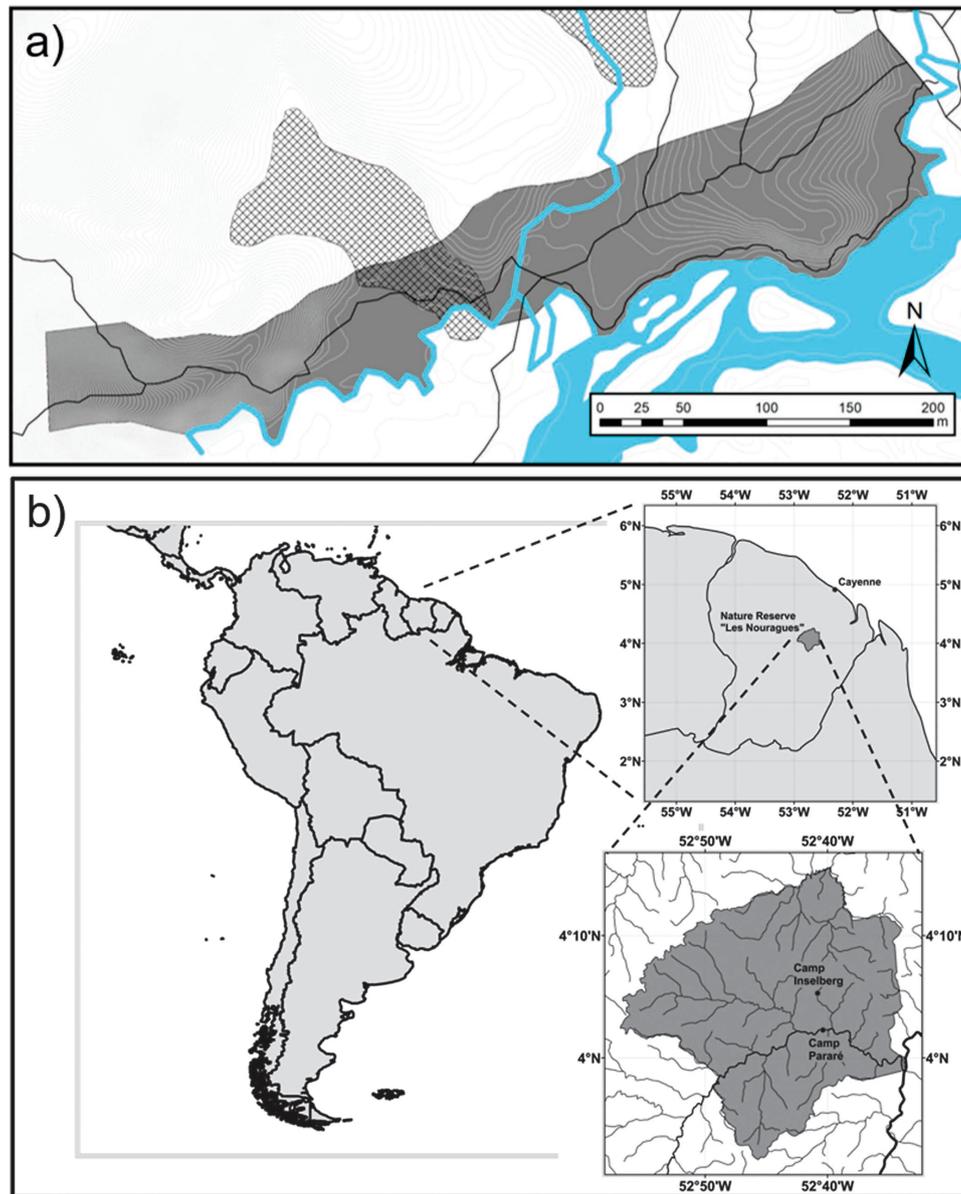


Figure 3. Schematic maps showing (a) location of the study plot (grey area); trails as thin black lines, thin grey lines indicate 50 cm elevation isoclines, cross hatched areas show palm swamps, blue areas show the river Arataye with islands and affluent creeks, and (b) location of the study area in French Guiana, taken from RINGLER et al. (2016) under a creative commons license (CC BY 3.0; <https://creativecommons.org/licenses/by/3.0/legalcode>).

We created encounter histories for each individual, indicating its presence or absence during each survey. We constructed four different models with time-dependent probability of entry, allowing survival (ϕ) and capture probabilities (p) to vary with time (t) or being constant over time (\cdot): (1) a global, fully time-dependent model $\{\phi(t), p(t), \text{pent}(t)\}$, (2) a model with time-dependent survival and constant capture probability $\{\phi(t), p(\cdot), \text{pent}(t)\}$, (3) a model with constant survival and time-dependent capture probability $\{\phi(\cdot), p(t), \text{pent}(t)\}$ and (4) a model with constant survival and capture probability $\{\phi(\cdot), p(\cdot), \text{pent}(t)\}$. The sin-function was used for capture and survival probabilities, the multinomial-logit link-function was used for the probability of entrance (pent) and the log-function was used for the super-population (N). We used the goodness-of-fit (GOF) test of the integrated 'Release' function of 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 assumptions was quantified as the quotient of χ^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.

Site fidelity and movement. To assess site fidelity, we measured pairwise distances between the initial and subsequent recapture locations for all individuals that we recaptured at least twice. For all individuals we calculated median distances for robustness against occasional long movement outliers. We pooled observations from 2010 and 2011 since there was no difference in median distances between the two years ($N_{2010, 2011} = 29, 65$, Mann-Whitney $U = 897$, $p = 0.712$). To analyse movement behaviour, we measured the day-to-day distances for each individual by converting capture location to individual trajectories with the 'Polylines from Points' function of XTools Pro 20.0 for ArcMap (Data East 2003–2021). Then, we split the trajectories in segments with the 'Split Line at Vertices' tool of ArcMap, and used the 'Calculate Geometry' function of Xtools to obtain segment lengths. To calculate the average daily movement, we then divided the distance between consecutive points by the number of days between these observations and calculated median values for each individual and the median of the medians across all individuals. We pooled observations from 2010 and 2011 since there was no difference in median daily distances between the two years (Mann-Whitney $U = 734$, $p = 0.11$).

To study a possible effect of size on movement, we calculated the correlation between body size and the total distance moved by individuals, as well as the median daily distance moved and the distance between the initial and consecutive locations. For individuals from 2010 that we recaptured in 2011, we calculated year-to-year displacement as the distance between the median centres of each individual's set of observations points, which we obtained via the 'Median Center' tool of the 'Spatial Statistics' tool-

box in ArcMap. We calculated all distances in ArcMap from projected data (WGS 1984, UTM Zone N22).

Home ranges. We calculated home ranges for individuals with ≥ 3 captures as minimum convex polygons (MCP) (MOHR 1947) (1947), using the 'Minimum Bounding Geometry – Convex Hull' tool in ArcMap. This simple approach to home range estimation creates a convex polygon encompassing all locations of an individual. It is widely used for simplicity and comparability with older studies but tends to overestimate home range size depending on spatial outliers (GAUTESTAD & MYSTERUD 1993, SEAMAN et al. 1999). We pooled observations from 2010 and 2011, as they were not significantly different (Mann-Whitney $U = 368$, $P = 0.06$) To analyse the spatial distribution of individuals, we calculated the nearest neighbour distances (NND) from the median centres of each individual's set of observation points in ArcMap.

Results

Captures

In 2010, over a study period of 35 days, we found 66 males in 227 captures, with a median recapture interval of 3 days (median of individual medians; range: 1–26). However, due to logistic constraints, we obtained spatial data only for 136 captures of 64 individuals. Males were captured on average 3.4 times ($SD = 2.3$, range: 1–11). Fifteen toads (23%) were captured only a single time, while 51 toads (77%) were captured at least twice, 19 (29%) at least five times, but only a single one (2%) was recorded more than ten times. Of the 64 males with GIS data, 29 (45%) were located at least twice, allowing for the analysis of movement, and 20 (31%) were located at least three times, allowing for home range analysis (MCPs, see below).

In 2011, over a study period of 27 days, we found 81 males in 557 captures, including nine survivors from the previous year, with a median recapture interval of 2 days (median of individual medians; range: 1–16). In 2011, the recapture rate was higher than the year before. Individual males were captured on average 6.8 times ($SD = 5.7$, range: 1–24). Sixteen toads (20%) were captured only a single time, while 65 toads (80%) were located at least twice, 45 (56%) at least five times, and 19 (23%) at least ten times. Forty-five of the 557 observations in 2011 were from complementary nocturnal surveys over four days at the end of our study. During that time, we found 22 males from 21:27 h to 22:56 h.

Details of captured individuals and recapture rates per day are illustrated in Figure 4, demonstrating that new individuals were captured mainly in the beginning of each study period. The maximum number of daily captures was 20 individuals in 2010 and 32 in 2011 (median 5 and 20, respectively). Only in 2010, on 3 days of the first quarter of the study period, we did not find any toads at all.

In 47% of all encounters of both years ($N = 784$), we detected toads when they were calling, while other encounters were either by chance or when checking loca-

tions where toads had been found previously (Fig. 5). Calling activity was highest in the morning, and we also had the impression that calling activity increased after rainfall. We encountered the vast majority of toads sitting on veg-

etation, but in a few cases, we observed individuals while moving on the ground or climbing. We hardly recorded any interactions between individuals; only in six encounters we found males overtly fighting.

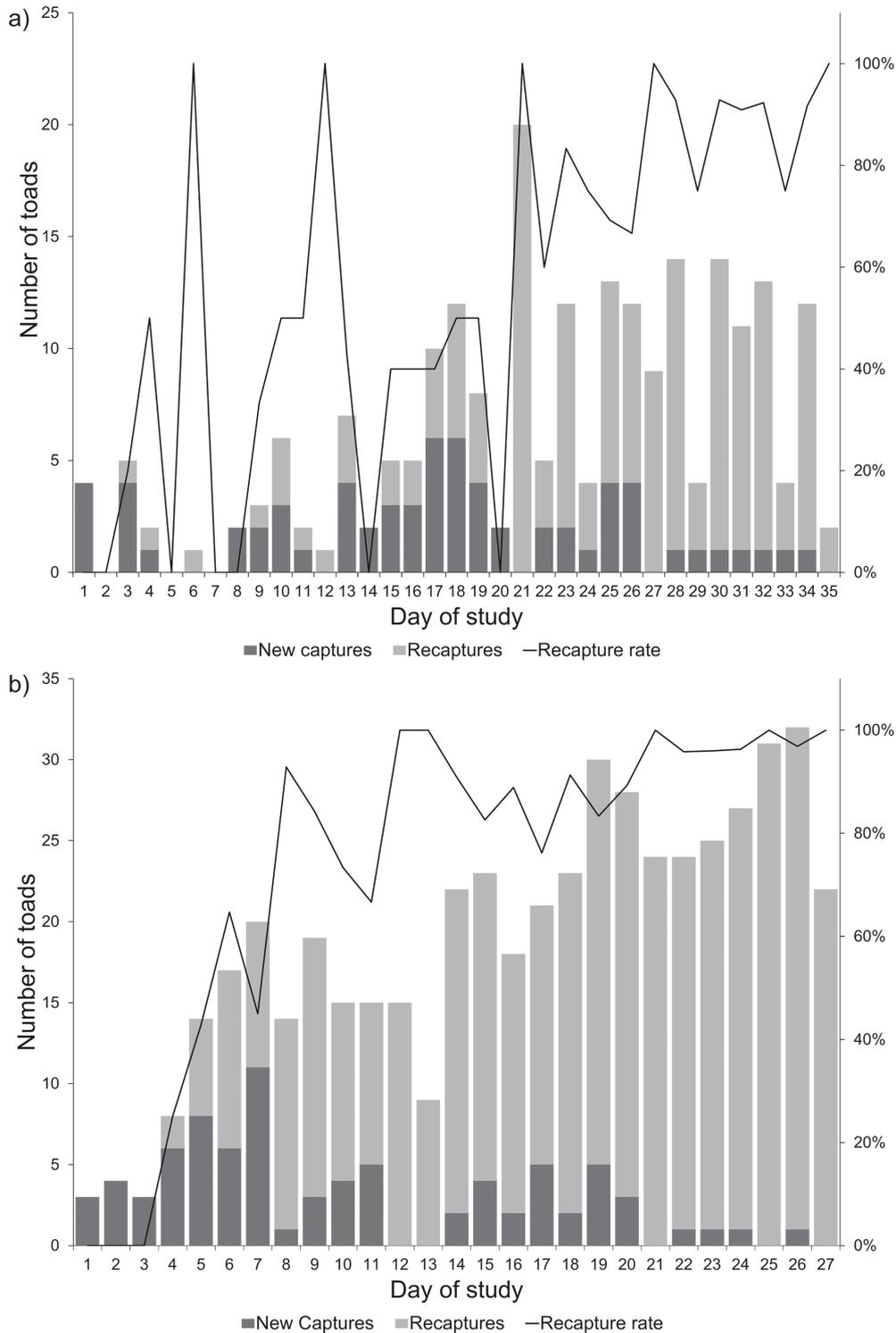


Figure 4. Daily captures of males during the study periods of 2010 (a) and 2011 (b). Bars indicate daily captures, with dark grey indicating new and light grey indicating recaptured individuals; lines show recapture rates.

Population size estimates

The POPAN model yielded population size estimates of 80.78 (SE = 5.71, 95% CI = 70.34–92.77) and 89.26 males (SE = 3.38, 95% CI = 82.87–96.14) for the two consecutive years, respectively. This corresponds to estimated population densities of 20.2 and 22.3 individuals/ha for the study plot in 2010 and 2011, respectively. The area of the MCP containing all capture points was 2.94 ha with corresponding estimated population densities of 27.5 and 30.4 individuals/ha in 2010 and 2011, respectively. Following the AICc for small sample sizes, the model with time-dependent survival, capture, and entry probability performed best for 2010. For 2011, the model with constant survival, and time-dependent capture and entry probability was best (Table 1). GOF test results for the global model ($\phi(t)$, $p(t)$, $\text{pent}(t)$) revealed an appropriate fit of data for both 2010 and 2011. TEST 2 of release, which tests for homogeneous capture probability among individuals, was neither significant for the first ($\chi^2 = 38.665$, $df = 37$, $p = 0.394$) nor for the second study period ($\chi^2 = 63.622$, $df = 58$, $p = 0.285$), suggesting no behavioural response of individuals to getting captured (cf. PRADEL 1993). TEST 3, which tests for equal survival probability of individuals, likewise was not significant in any of the two years (2010: $\chi^2 = 13.256$, $df = 28$, $p = 0.991$; 2011: $\chi^2 = 34.452$, $df = 33$, $p = 0.398$). Corresponding to these results, pooled TEST 2 and TEST 3 supported an adequate fit of the global model (2010: $\chi^2 = 51.921$, $df = 65$, $p = 0.88$; 2011: $\chi^2 = 98.074$, $df = 91$, $p = 0.288$). The estimation of overdispersion (\hat{c}) indicated that data were not over-dispersed and thus the assumptions of independence and homogeneous survival probability of individuals were neither violated in 2010 ($\hat{c} = 0.799$) nor 2011 ($\hat{c} = 1.08$).

Spatial behaviour

Atelopus males were not evenly distributed and showed three areas with higher male density in the proximity of the smaller creeks in the western part of the study plot, while a few individuals were spaced out along the river Arataï in the eastern part (Fig. 6). The patterns of occurrence did not differ much between the two years; however, in the easternmost part of the study plot we found toads only in 2010.

The median distance of the median centres of activity of toads to the next creek or the river Arataï was 9.55 m (range: 0–88.65 m; $N = 145$; Fig. 7). All toads that we found further than 35 m from water were captured on the hill at the western edge of the study plot (Fig. 5). Although most parts of the study plot were relatively flat with altitudes between 29 to 34 m a.s.l., these distances are conservative approximations since they were calculated in projected view and not along the slope of the terrain. Hence, distances to the creek on the ground are larger, in particular for individuals captured on the hill. We found no correlation between the SUL and distances to water (Spearman's $r_s = -0.027$, $p = 0.746$).

During the day (07:30–18:00 h; $N = 739$), we detected toads mostly on trees (38.6%) and shrubs (17.3%), some used also lianas (16.4%) and logs as perches (9.9%). We found toads less often in the leaf litter (6.1%) or on rocks (2.6%), and only exceptionally on roots (2 encounters) and palms (2 encounters). Information on the encounter substrate was not recorded for 64 captures (8.7%), however. We observed toads from the ground level up to 2.7 m height, with a median height of 70 cm above the ground (median of individual medians; $N = 147$, range: 0–175 cm;

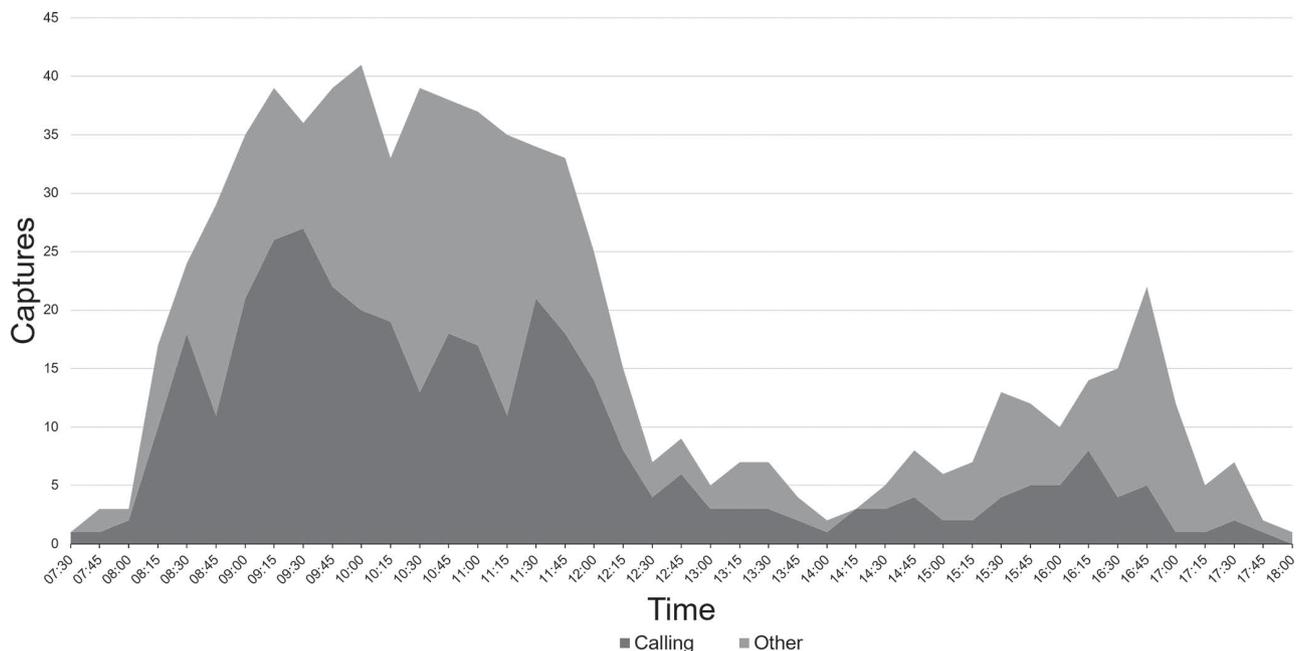


Figure 5. Hourly captures of males during both study periods from 07:30–18:00 h ($N = 739$; additional nocturnal sampling excluded). Dark grey indicates captures where the male was found calling, light grey indicates all other captures.

Table 1. Models constructed with POPAN and sorted by AICc value.

Year	Model	AICc	Δ AICc	AICc weights	Model likelihood	Number of parameters	Deviance
2010	$\phi(t), p(t), pent(t)$	1026.4	0.00	0.9379	1.0000	49	355.84
	$\phi(\cdot), p(\cdot), pent(t)$	1031.83	5.43	0.0621	0.0663	15	454.82
	$\phi(t), p(\cdot), pent(t)$	1105.01	78.61	0.0000	0.0000	50	431.26
	$\phi(\cdot), p(t), pent(t)$	1136.26	109.86	0.0000	0.0000	80	342.16
2011	$\phi(\cdot), p(t), pent(t)$	1675.56	0.00	0.9998	1.0000	39	893.87
	$\phi(\cdot), p(\cdot), pent(t)$	1692.87	17.31	0.0002	0.0002	19	1653.3
	$\phi(t), p(t), pent(t)$	1712.65	37.09	0.0000	0.0000	63	1568.4
	$\phi(t), p(\cdot), pent(t)$	1738.86	63.31	0.0000	0.0000	45	1639.86

Fig. 8). There was no correlation between SUL and diurnal perch height (Spearman's $r_s = -0.0196, p = 0.815$).

During the four nocturnal surveys, we recorded 22 males in 45 encounters. Toads were resting mainly on leaves of trees (53.3%) and shrubs (26.7%), while only 8.9% of the encounters were on rocks, 4.4% on lianas and logs, respectively, and 2.2% on roots. During the night, we found toads sitting significantly higher than during the day (mean of individual means = 118 cm, range: 22–200 cm; t-test, $t = 4.3572, p < 0.001$). The nocturnal encounter locations were in close vicinity of the diurnal perches, with a median distance of 54.7 cm to the median centres of activity (median of individual medians, range 3.9–219.7 cm). There was no correlation between SUL and nocturnal perch height (Spearman's $r_s = 0.205, p = 0.361$); also, diurnal and nocturnal perch height was not correlated (Spearman's $r_s = 0.33, p = 0.134$).

Site fidelity and movement

For 94 males (64%) we had at least 2 captures during one of the study periods, generally close to their initial capture locations. The median distance between the first capture and all further recapture locations of each individual was 2.03 m (median of individual medians, range 0.01–28.5 m). Although we found several individuals quite far from their initial capture location, 36.3% of the recaptures ($N = 548$) occurred within < 1 m and 70.6% within < 5 m from the initial sighting. Only 4.3% of the recaptures were more than 15 m from the initial location (Fig. 9).

More than half of the males (55.6%) moved less than 1 m per day, 28% between 1–5 m, and only 6.5% of the males moved more than 5 m (Fig. 10). The individuals with little movement were often recaptured on the exact same branch

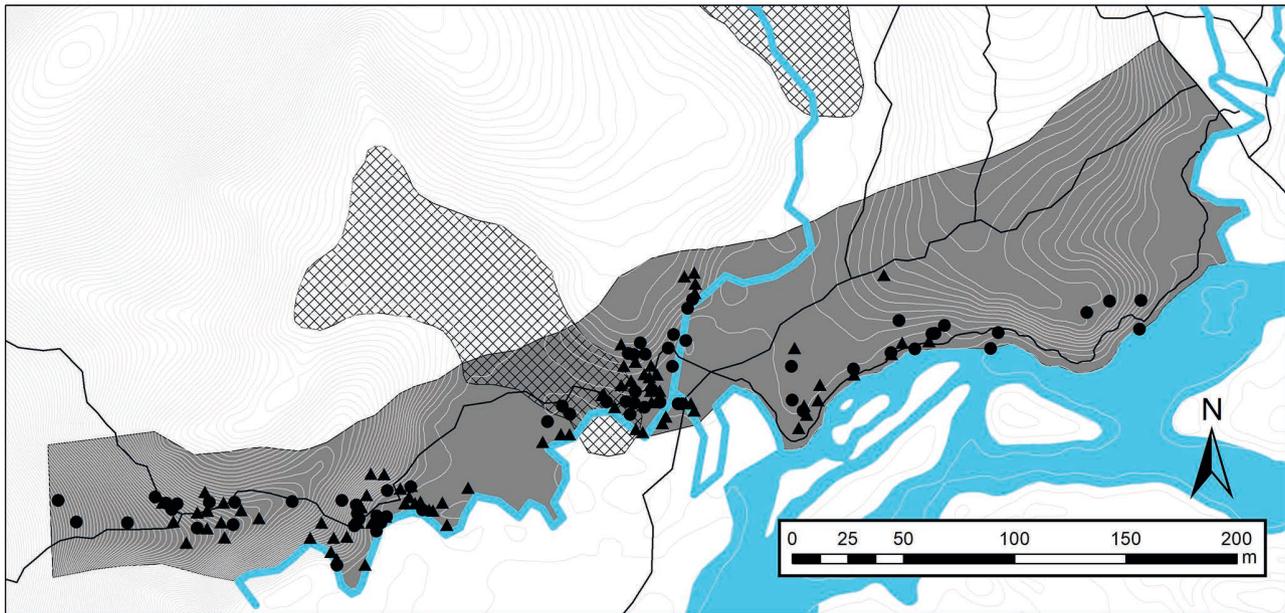


Figure 6. Schematic map showing locations of all males ($N = 145$; 2 males without spatial data excluded) encountered during both study periods. Shown are median annual centres of activity, based on all captures per individual. Circles refer to males encountered in 2010, triangles to those in 2011, trails are shown as thin black lines, thin grey lines indicate 50 cm elevation isoclines, cross hatched areas show palm swamps, blue areas show the river Arataye with islands and affluent creeks.

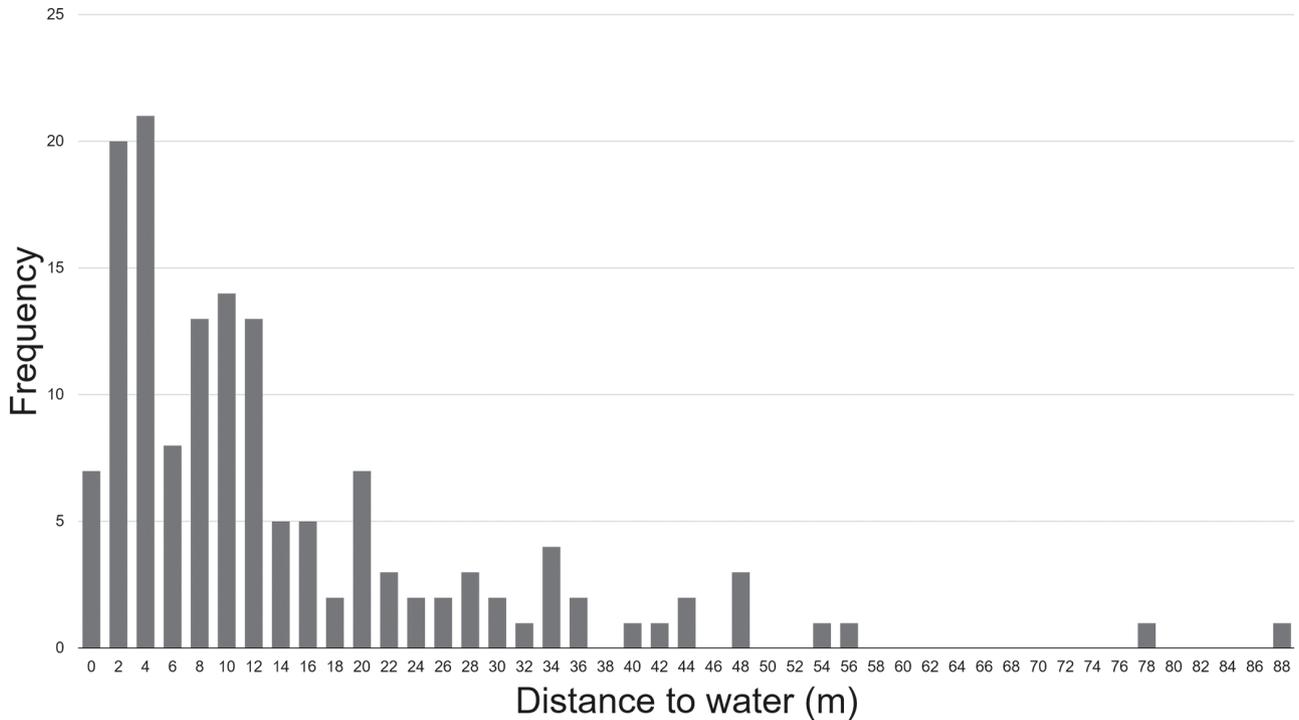


Figure 7. Histogram of the median distances of males to the creek or the river Arataye (N = 145).

or axil of a tree or shrub, others were found on the same plant, but changed positions horizontally along a branch, or vertically along the tree trunk. Males with median daily movements of more than 2 m had a median number of only 2 captures (range: 2–5, N = 9), indicating that they were rather transient individuals that were found while migrating through the study plot.

Males moved a median distance of 0.49 m per day (range: 0–7.13; median of individual medians), with single movement observations ranging from 0–22.75 m per day (median = 0.4 m per day, N = 497). The median time span between consecutive captures of the individuals was 2 days (range: 1–18 days).

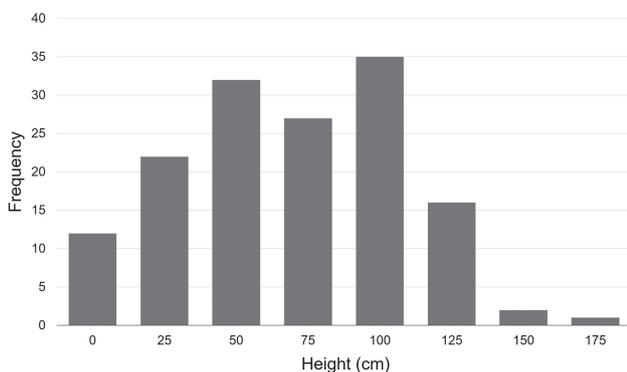


Figure 8. Histogram of the median encounter heights of individual toads during the day (N = 147).

Correlation tests revealed that body size did not affect movement behaviour; there was neither an effect on the total distance moved by the toads during the entire study period (Spearman's $r_s = -0.108$, $p = 0.303$) nor on the median daily moved distance (Spearman's $r_s = 0.125$, $p = 0.233$). Moreover, the distance between the initial and consecutive captures did not depend on body size ($r_s = 0.046$, $p = 0.659$).

The nine individuals that we captured in both years moved a median distance of 15.3 m (range: 2.86–81.01 m) between years. Three of them were found within a range of 10 m of their capture locations in the previous year.

Home ranges

For 72 individuals with at least 3 capture points, we calculated MCPs. These home ranges were relatively small (median area: 2.19 m²), but their size differed among individuals remarkably between 0.00001–214.41 m². Male body size did not correlate with home range size (Spearman's $r_s = -0.029$, $p = 0.81$). In 2010, we did not find any home range overlap. In 2011, MCPs of 19 individuals were overlapping. In most cases, the overlap was related to pairwise intersection of home ranges; only in one situation we observed the overlapping of home ranges of 4 individuals. For the males with overlapping home ranges, the median percentage of the home range area they shared with neighbours was 15.78% (range: 0.24–96.91%).

The median nearest-neighbour-distance (NND) between males was 5.46 m (range: 0.1–31.42 m, $N = 145$). There was neither a significant correlation between NND and SUL (Spearman's $r_s = 0.013$, $p = 0.874$) nor between NDD and home range size (Spearman's $r_s = 0.1$, $p = 0.4$).

Anecdotal observations of females

Although we did not actively search for *Atelopus* females in the course of our study, in 2010 three other teams of researchers, working on other species in adjacent areas (see

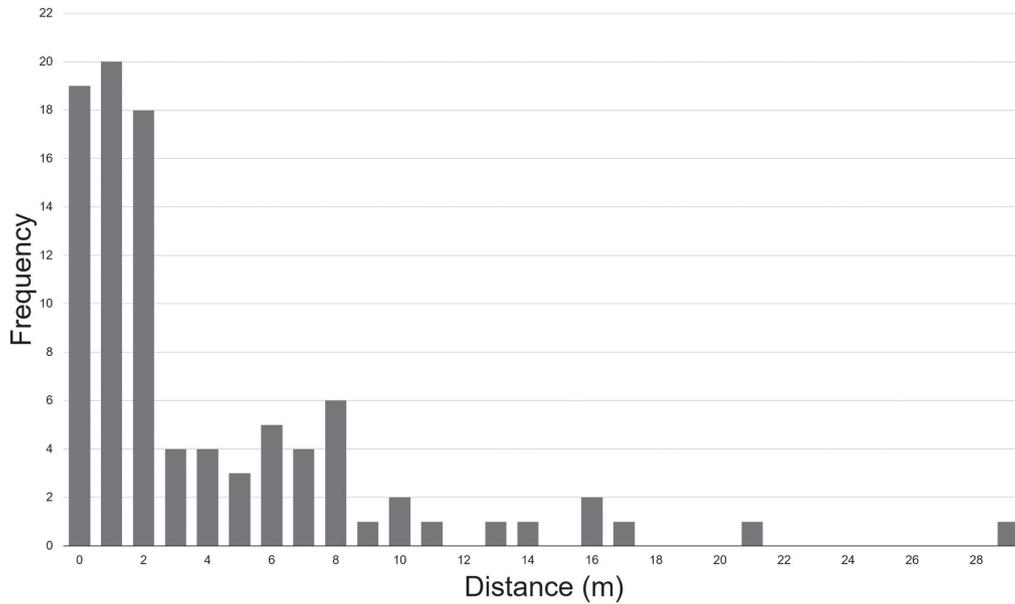


Figure 9. Distribution of individual median distances between the first and all subsequent captures of all males that were captured at least twice ($N = 94$).

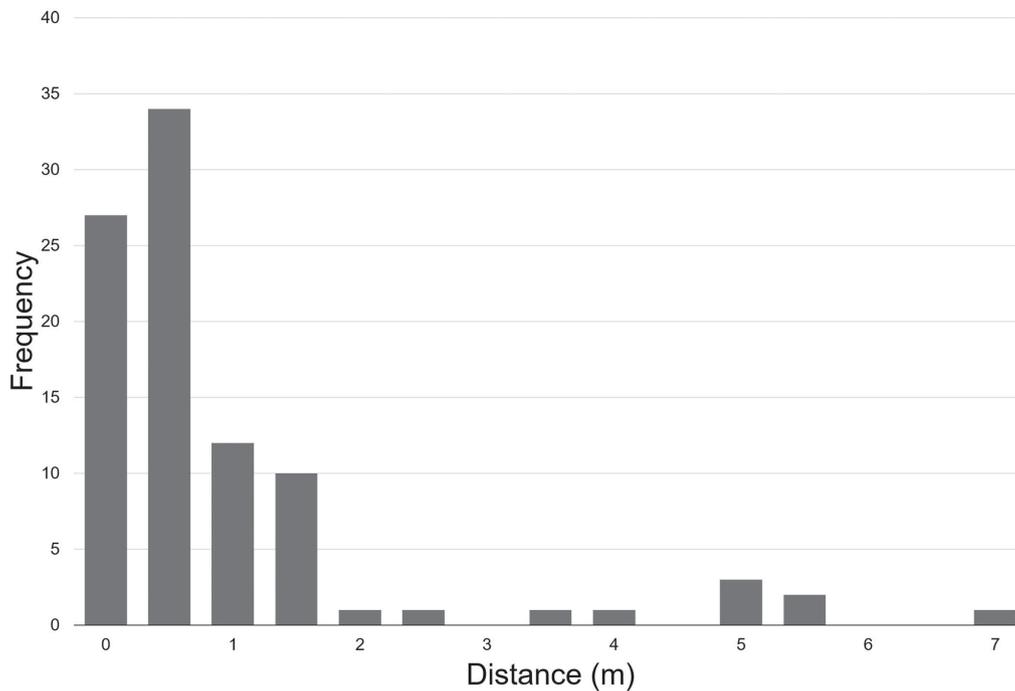


Figure 10. Distribution of median individual day-to-day movements of males that were captured at least twice ($N = 93$; one individual was only found twice on the same day).

BÖHM 2013, ROJAS & ENDLER 2013, ERICH et al. 2015), and our group made several anecdotal observations of 12 females in total (Fig. 11). Most females were found along regularly used trails in the area. Nine females were only encountered a single time, while for three individuals we made two observations. Only one female was encountered inside, and one only 2 m outside our study plot. The average distance of these females to our study plot was 427 m (range: 0–1157 m). Of the three females with two observations, two moved 1.47 m from and 1.86 m towards our study plot over the course of 4 and 2 days, respectively. One female moved over 338 m from our study plot over the course of 6 days. Eleven females were found on the ground in plain forest while only one female was found on a tree, directly at a creek. No female was found in amplexus with a male. In 2011, neither we nor other researchers working in the area during our study period found any *Atelopus* females.

Discussion

Male *Atelopus* in the Nouragues Reserve are diurnal and aggregate along running water (median distance: 9.55 m) over long periods, when they defend relatively small home ranges (median area: 2.19 m²). They show site fidelity (median distance between initial and subsequent recapture locations: 2.03 m) and have markedly limited movement (< 1 m per day in 55.6% of observations). Individuals were mainly found on plants at a median height of 70 cm above ground and only seldom at ground level. At night, most males were located near the sites where they were found during the day (median distance: 54.7 cm) but significantly higher up in the vegetation (mean height: 118 cm). None of the studied parameters correlated with body size (SUL).

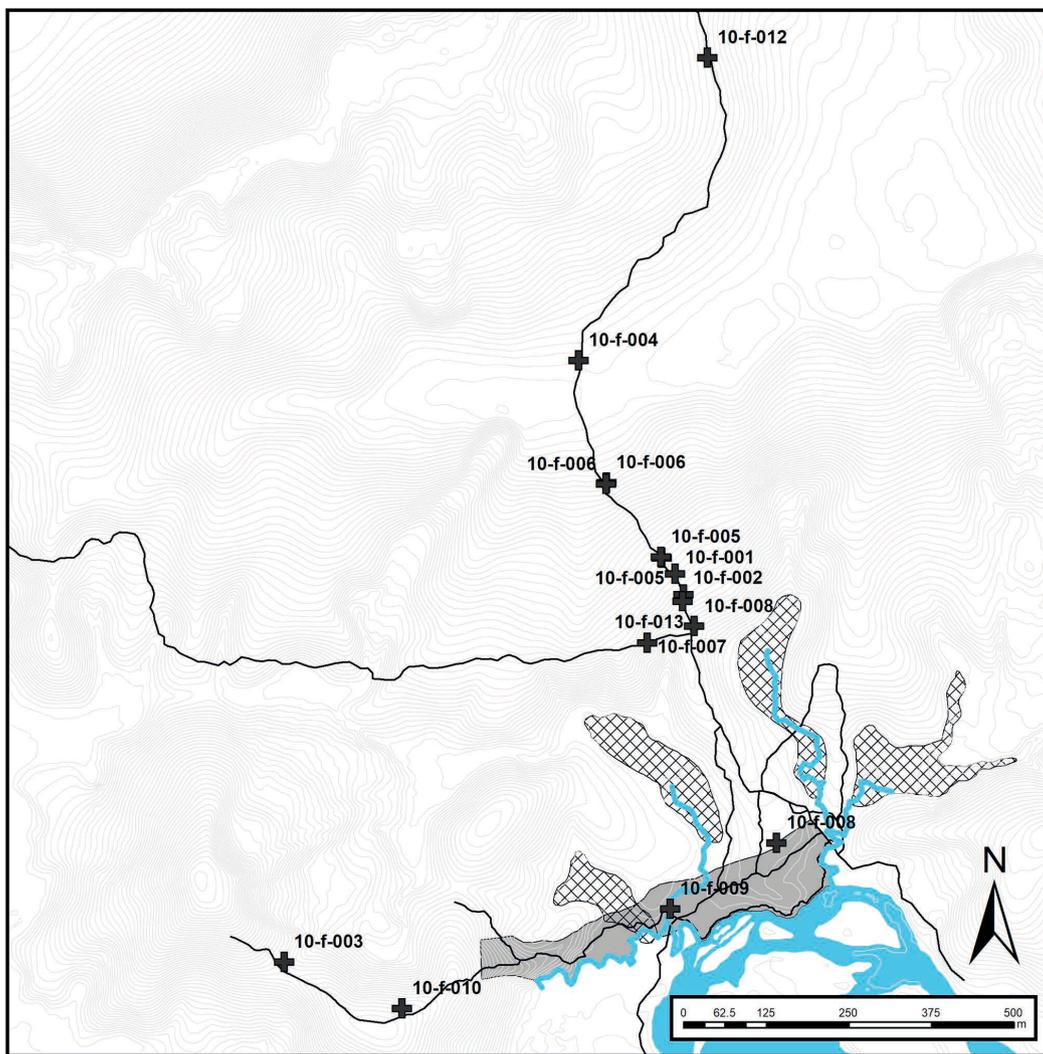


Figure 11. Schematic map showing encounter locations of 12 females (crosses) that were found during our study period in 2010. Black lines indicate trails, thin grey lines indicate 2 m elevation isoclines, cross hatched areas show palm swamps, blue areas show the river Arataye with islands and affluent creeks.

Captures and population density

The low number of newly found individuals towards the end of both study periods (Fig. 4) indicates that we had recorded most individuals that were present in the study plot, which suggests robustness of our data for the performed analysis. The relatively low number of individuals found only once ($\leq 23\%$) is similar to the findings of LUGER et al. (2009) on the related *A. hoogmoedi* in Brownsberg Nature Park, Suriname. In the Central American *A. varius*, CRUMP (1986) recorded both strongly resident and transient individuals, a concept that might well apply to the *Atelopus* populations of our study and of LUGER et al. (2009).

While several *Atelopus* species are known for their longevity (LÖTTERS 1996), it has been shown that their life expectancy can be considerably reduced by a pathogen, the invasive, lethal chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*), e.g. *A. cruciger* in a coastal forest in Venezuela (LAMPO et al. 2012). These authors also suggested that migration did not play a role for observed fluctuations in their population, because of the absence of nearby streams as origin or destination of potential transient individuals. Single observations in this study might therefore be the result of high mortality in this population, related to *Bd*. In our study population, transient individuals seem more plausible because of the relatively smooth relief and several other creeks within migration distance to our study plot. Yet, *Bd* is known from this area (7.4% prevalence in *A. flavescens*; COURTOIS et al. 2015) and we cannot rule out a possible effect on our study population.

The differences in the recapture rates in 2010 and 2011 can be explained by a slightly higher sampling effort and our increased familiarity with the study area and species in the second year. In the first year, we assessed the population for the first time with two consecutive field workers (ML, PW). In 2011, we mostly knew about the preferred locations of the males in the habitat, and one field worker (TH) was present throughout the entire study period and was supported by one to three field assistants.

Apparently linked to this circumstance, capture probabilities (POPAN) in 2011 were slightly higher than in 2010. A more detailed look at the parameter estimates for the survival and capture probabilities from the POPAN model revealed that the capture probabilities of individuals varied temporally and were generally low, while the survival probabilities were high. Generally, population estimates have a high accuracy when both capture and survival probabilities are high (cf. WAGNER et al. 2011), which suggests an intermediate accuracy of our population estimates. Nevertheless, the estimated population sizes for 2010 and 2011, 81 and 89 individuals, respectively, only slightly exceeded the actual numbers of captured males. This suggests a sampling coverage of 81.5% of the entire male population during the first and 91% during the second study period. This is in contrast to the study of LAMPO et al. (2012), who demonstrated that in *A. cruciger* visual counts were not reliable to assess population size/abundance, compared to estimates from population models (POPAN). However, in their study they as-

essed an *Atelopus* population with 12 mark-recapture sessions over the course of three years, with nine sessions in the second year. This sampling regime is strikingly contrasting to our approach where we sampled on 35 and 27 consecutive days, and where therefore a much better match between encounters and estimators in any year can be expected.

Based on our data, estimated male density ranged between 20.2 and 22.3 males/ha in the study plot and between 27.5 and 30.4 males/ha in the area (MCP) where toads were found, with a median nearest-neighbour-distance between males of 5.46 m. In other congeneric species, even higher densities have been reported. LUGER et al. (2009) recorded 19 males in only 1,000 m² for the related *A. hoogmoedi* in another lowland rainforest in Suriname. Likewise, just along a 130 m stream transect CRUMP (1986) counted at least 45 individuals of both sexes of the Central American *A. varius*, and DOLE & DURANT (1974) reported 20 males and 37 females for a 1 ha study plot in *A. carbonerensis* from a Venezuelan cloud forest. LAMPO et al. (2012) pointed out that density can be highly variable in *A. cruciger* from a Venezuela lowland forest, ranging 0.005–0.057 toads/m², due to season, death rates and recruitment.

Spatial distribution

Toads in our study were strongly associated with riverine habitat, like – at least for certain periods of the year – in many other harlequin toad species (LÖTTERS 1996). Notably, although males occupied sites close to running water, the immediate proximity (i.e., < 2 m distance; Fig. 7) was not the most preferred, similar to males of the related *A. hoogmoedi* (LUGER et al. 2009). Creek segments were not occupied equally in our study plot, and although microhabitat quality does not influence site fidelity in other *Atelopus* (*A. varius*; CRUMP 1986), we hypothesise that microhabitat heterogeneity could play a role in our study. For example, the absence of males between the two areas of higher density within the study plot probably can be explained by the swampier conditions (cf. Fig. 5) that might



Figure 12. Flooding of the study plot in 2010, which occurred after heavy rainfalls during a single night. Photo: MAX RINGLER.

be generally unfavourable to *Atelopus*. Also, profitable foraging sites, shelter availability, or advantageous calling positions cannot be expected to be evenly distributed. Aggregated occurrence of calling males could also be a response to a female-initiated mating behaviour, e.g. orientation towards calling males, which would be facilitated by larger calling choruses (WELLS 2007).

In our study we found toads predominantly on living plants (trees, shrubs etc.) at < 1 m above ground rather than in the leaf litter, similar to observations in the phylogenetically related Guianan *A. hoogmoedi* by LUGER et al. (2009). Another study revealed that this species mostly exploits the leaf litter during the day (13:00 hrs), while higher vegetation up to 130 cm above ground was almost exclusively used at night (18:00 hrs) (NICOLAÏ et al. 2017). Similarly, *A. laetissimus* from a montane forest in the Sierra Nevada de Santa Marta (Colombia) was found on rocks and decaying leaves during day time and plants at higher positions during night time where it even forages (GRANDA-RODRÍGUEZ et al. 2008, RUEDA-SOLANO & WARKENTIN 2016). Our observations did not show a relevant amount of leaf litter exploitation during the day, but we cannot not rule out such behaviour related to season or local conditions (cf. NICOLAÏ et al. 2017), as we did not specifically investigate circadian activity variation. Like for other *Atelopus*, in the population studied we confirm a strong tendency of climbing to significantly higher sites for sleeping during night-time. This behaviour can be interpreted as predation evasion, as proposed for the Panamanian *A. zeteki* (LINDQUIST et al. 2007). It may also minimise the risk of being washed away by sudden floods, as it has been proposed for *A. hoogmoedi* (LUGER et al. 2009). Such rapid flooding occurs in the lower parts our study plot and was observed by us in 2010 (Fig. 12).

Site fidelity and movement

According to our results, male toads showed high site fidelity during each study period, with 70% of them having a movement radius of < 5 m. The observed distances of movement mostly correspond to changes between neighbouring trees. Between the two study years, 3 of 9 survivors from 2010 were found in nearby sites in 2011 (< 10 m distance from initial site). Site fidelity is a common behavioural trait in *Atelopus* species (SEXTON 1958, DOLE & DURANT 1974, CRUMP 1983, 1986, 1988, LINDQUIST & HETHERINGTON 1996, LÖTTTERS 1996, KARRAKER et al. 2006, LINDQUIST et al. 2007, LUGER et al. 2009, NICOLAÏ et al. 2017). Various benefits of site fidelity are known in general, for example familiarity with the environment and habitat features, like advantageous shelters, calling sites, or escape routes (BAKER 1978). In our study species, preferred perching locations could improve call transmission to serve in attracting females. As *Atelopus* males actively approach females for amplexus (LÖTTTERS 1996), males on high quality perches probably can spot females earlier when they approach calling aggregations (cf. LUGER et al. 2009 for sim-

ilar considerations in *A. hoogmoedi*). As we did not find any females in our study plot in both years, we assume that males maintain and defend spatial resources at the breeding sites also outside of the breeding season, or at least long before the females arrive.

Home ranges

Males in our study maintained markedly small home ranges (median: 2.19 m²). Although maximum home range size was > 200 m², our results suggest that in our study species home ranges are smaller than in the closely related *A. hoogmoedi* (LUGER et al. 2009; mean > 38 m²) or in *A. carbonerensis* (DOLE & DURANT 1974; mean: > 32 m²). It is important to note that toads also clearly exploited the vertical dimension of the habitat and used elevated sites on trees and shrubs up to 3 m above ground both during diurnal activity and nocturnal resting. Small planar home ranges in combination with pronounced vertical behaviour indicate that for males of the studied population, as for other climbing species, probably a vertical/3D concept of their home range/territory might be more appropriate to capture the spatial behaviour of the species (cf. CHANDLER et al. 2020, BASHAM et al. 2022). However, the number of location fixes per individual precluded a meaningful 3D home range analysis in our study. Probably, even single trees could be considered as the territory of individuals, with only little movement between trees – resulting in the small planar home ranges that we observed. Males might only leave trees for feeding, when disturbed by a predator or a conspecific territorial intruder, or when in amplexus with a female and on the way to the aquatic breeding site. This is corroborated by the observation that we found only little to no home range overlap among males in our population.

Conclusive remarks in the frame of *Atelopus* reproductive biology

Generally, it is well understood that harlequin toads aggregate along streams for reproduction, that eggs are laid in strings and that larvae are stream-adapted, belonging to the gastromyzophorous type (LÖTTTERS 1996). This also includes Guianan *Atelopus* (LESCURE 1981, BOISTEL et al. 2005a). In line with the lek mating strategy known in many anurans (WELLS 2007), *Atelopus* males commonly outnumber females and perform female guarding (e.g. SEXTON 1958, DOLE & DURANT 1974, JASLOW 1979, CRUMP 1986, 1988, LINDQUIST & HETHERINGTON 1996, LÖTTTERS 1996, KARRAKER et al. 2006, LINDQUIST et al. 2007, LAMPO et al. 2012, ROCHA USUGA et al. 2017, RUEDA-SOLANO et al. 2022).

Atelopus carbonerensis from a cloud forest in the Venezuelan Andes is one of the best studied harlequin toad species. It has a strictly defined breeding season in the short ‘veranillo’ dry season from May to July. Outside

this period, both sexes maintain home ranges in the forest several hundred meters away from water (SEXTON 1958, DOLE & DURANT 1974, JASLOW 1979, CRUMP 1983, 1986, 1988, LINDQUIST & HETHERINGTON 1996, LÖTTTERS 1996, KARRAKER et al. 2006, LINDQUIST et al. 2007, LAMPO et al. 2012). The reason might be that during ‘veranillo’, the stream current is less and the risk for adults and tadpoles to be washed away is therefore reduced, as also observed in other montane harlequin toads (LYNCH 1986, LÖTTTERS 1996). This risk would allow *A. carbonerensis* males to directly migrate to streams only as late as at the end of April or early May to fight for advantageous sites to spot and get into amplexus with arriving females, almost about the same time when females arrive. As a result, when possible, males amplex females already long before migration starts to monopolize them, occasionally already in December. Amplexus in this species can last to at least 125 days. With up to 135 days, amplexus can be even longer in *A. laetissimus* from the Sierra Nevada de Santa Marta in Colombia (SEXTON 1958, DOLE & DURANT 1974, JASLOW 1979, CRUMP 1983, 1986, 1988, LINDQUIST & HETHERINGTON 1996, LÖTTTERS 1996, KARRAKER et al. 2006, LINDQUIST et al. 2007, LAMPO et al. 2012, RUEDA-SOLANO et al. 2022). This is coupled with high costs in terms of energy loss, as males are not feeding while in amplexus.

Lowland species of *Atelopus*, as the one studied here, exhibit a different female guarding strategy. According to BOISTEL et al. (2005a), reproduction in the *A. flavescens* complex in French Guiana takes place during the heavy rains in April and May when females arrive at streams – and not during drier periods of the year. A simple explanation might be that in lowlands, stream currents are generally lower than in montane regions and that streams may entirely dry out during dry seasons. This circumstance allows males to occupy and defend advantageous sites to spot arriving females a considerable time before females arrive (as also observed in the similar *A. hoogmoedi*; LUGER et al. 2009, NICOLAÏ et al. 2017). Amplexus therefore could be much shorter than in e.g. *A. carbonerensis* or *A. laetissimus*. Indeed, at least under captive conditions, amplexus in the *A. flavescens* complex was reported to last only 34 days (LÖTTTERS 2007, GAWOR et al. 2012). In conclusion, we hypothesize that energy investment between territorial advertisement and female guarding through a relatively short amplexus is more balanced in lowland species, reproducing during rainy seasons, compared to montane congenetics, reproducing during dry short ‘veranillo’ seasons.

Costs for reproduction in male *Atelopus* were also studied by ROCHA USUGA et al. (2017) in *A. laetissimus* from the Sierra Nevada de Santa Marta in Colombia. In this species, survival of males is increased when breeding during extraordinary long dry seasons is prolonged. The authors suggested that in these conditions competition for females is less and thus energy investment is lower than in years with heavy rains and short breeding seasons.

There is limited information available on the life history of harlequin toads, which is in stark contrast to the urgent need to better understand these amphibians in the light of

the massive extinction threats they are facing. We here give insight into the biology of a lowland species suggesting within genus plasticity with regard to reproductive strategies, which we consider a relevant aspect when developing in situ and ex situ conservation measures.

CRedit author statement

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