

Site fidelity, home range behaviour and habitat utilization of male harlequin toads (*Amphibia: Atelopus hoogmoedi*) from Suriname: relevant aspects for conservation breeding

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Abstract. Recently, neotropical harlequin toads (*Atelopus* spp.) have undergone drastic population declines. Captive breeding has been suggested as a way to conserve harlequin frogs threatened by the amphibian chytrid fungus and global warming. A major problem is that little is known with regard to the natural history of *Atelopus* species. We studied male *A. hoogmoedi* site fidelity, home range and habitat utilization during the long rainy season (April to August) at Brownsberg Nature Park, Suriname. During this period, males and females occupy different habitats (i.e. streams versus forest). We studied male toads along a stream site. In total, 19 males were observed; relative abundance was 0.475 individuals per meter. Fourteen males were recaptured at the same site or its vicinity at least once and 12 maintained home ranges ($38.1 \pm 17.7 \text{ m}^2$ in size) for up to four months. However, male-male interaction was not observed. In the vicinity of streams, male *A. hoogmoedi* were perched $51.95 \pm 36.7 \text{ cm}$ above ground in dense understorey. In conservation breeding efforts, we recommend to keep sexes separately prior to mating and to simulate the rainy season. Because males occupy home ranges at the breeding site, reproductive success in captivity may be higher when females are moved to male containers (which should have some running water imitating a stream habitat). Low male density and home range size should be considered when populating tanks with males. Tanks for males and breeding should address that wild specimens were mostly found on low vegetation.

Key words. Anura, Bufonidae, ex situ conservation, habitat utilization, home range, site fidelity.

Introduction

Neotropical harlequin toads, genus *Atelopus* DUMÉRIL & BIBRON, 1841 (Bufonidae), comprise a group of more than 100 diurnal, slow-moving species, which aggregate along streams for reproduction (LÖTTTERS 1996). For almost two decades now, harlequin toads have dramatically declined throughout their geographic range (LA MARCA et al. 2005). According to the IUCN/Conservation International/NatureServe 'Global Amphibian Assessment', the genus is threatened with extinction with 81% of the species falling under the IUCN Red List category Critically Endangered (LÖTTTERS 2007). Reasons for these declines remain unknown in most cases, leading STUART et al. (2004) to use the term 'enigmatic' declines. Among others, the amphibian chytrid fungus (*Batrachochytri-*

um dendrobatidis) and anthropogenic climate change have been suggested to play a role (e.g. LA MARCA et al. 2005, POUNDS et al. 2006); however, others have disputed the link between climate change and outbreaks of chytridiomycosis (LIPS et al. 2008). The few harlequin toads with apparently stable populations (although in IUCN Red List categories Vulnerable or Endangered) include those from eastern Central America, the lower eastern Andes of southern Peru and adjacent Bolivia, the Amazon basin and the Guianas (<http://www.iucnredlist.org>; last accessed 15 May 2009).

Because some populations which had been stable until recently are currently undergoing dramatic declines, such as the Panamanian *Atelopus limosus* IBÁÑEZ, JARAMILLO & SOLÍS, 1995 and *A. zeteki* DUNN, 1933 (LIPS et al. 2006, K. ZIPPEL pers. comm.), we

fear that soon the entire genus *Atelopus* will become extinct (LA MARCA et al. 2005, LÖTTERS 2007). As advocated in the IUCN Amphibian Conservation Action Plan (ACAP), one measure to prevent amphibian diversity from irreversible loss is conservation breeding (GASCON et al. 2007). According to LÖTTERS (2007), any *Atelopus* species should be considered a candidate for ex situ conservation. There is an urgent need for information on natural history from the wild that can be applied to improve captive breeding. Only a few studies are available (reviewed in LÖTTERS 1996), mainly addressing spatial and temporal associations with a particular habitat. At the Monteverde cloud forest, Costa Rica, *Atelopus* sp. (cf. *varius*) aggregates along streams during the dry season (November–May) and disperses more uniformly during the rainy season. Individuals of both sexes exhibit site fidelity and maintain territories (CRUMP 1986, 1988, POUNDS & CRUMP 1989 – each as *A. varius*). In *A. carbonerensis* RIVERO, 1974 from humid forests in the Cordillera de Mérida, Venezuela, both sexes maintain defined home ranges throughout the year, except for the somewhat drier period (May to July) when individuals migrate to streams and reproduce (DOLE & DURANT 1974 – as *A. oxyrhynchus*). SEXTON (1958) observed migrations to streams in both sexes of *A. cruciger* LICHTENSTEIN & MARTENS, 1856 from coastal forests in Venezuela during the dry season (December to March), and proposed that some male *A. cruciger* are prolonged residents along streams. In Panama, *A. zeteki* aggregate along streams from late November/early December (the beginning of the mating season and the transition between the wet and dry seasons) to January (KARRAKER et al. 2006). Both sexes exhibit site fidelity (C. L. RICHARDS pers. comm.), with daily movements to and from elevated nocturnal sleeping positions (LINDQUIST et al. 2007). Male *A. pulcher* BOULENGER, 1882 from Andean Peru showed site-fidelity and both sexes aggregated along streams during reproduction in the dry season (May to

July, J.L. BROWN pers. comm.). However, not all species of *Atelopus* follow these temporal patterns, since for example *A. franciscus* LESCURE, 1974 from coastal French Guiana (BOISTEL et al. 2005) and *Atelopus* sp. cf. *spumarius* COPE, 1874 from near Iquitos, Peru (J.L. BROWN pers. comm.), reproduce during the rainy season. These observations suggest that tempo-spatial behaviour varies among the genus *Atelopus*, which is relevant for conservation breeding.

We studied *Atelopus hoogmoedi* LESCURE, 1974, a species widespread on the eastern Guiana Shield with seemingly intact populations (RUEDA et al. 2005, LUGER et al. 2008). The senior author's preliminary observations revealed that male *A. hoogmoedi* are permanently found along small streams, while females are encountered in forest at some distance from streams. We observed females migrating to streams in January 2003, at the start of the short dry season. We studied site fidelity, home range size and habitat utilization in males of this species along a small stream in Suriname during the rainy season. Further, the relevance of our findings for conservation breeding of *A. hoogmoedi* is discussed.

Material and methods

Field work

Field work was conducted at Brownsberg Nature Park, Suriname (Fig. 1). Established in 1970, the park currently encompasses 12,200 ha, i.e. most of Brownsberg Hill, a laterite range reaching 500 m elevation. The area is characterized by rugged terrain with evergreen forested steep slopes. The climate is seasonally tropical and humid with annual mean temperature of about 26°C and annual bimodal rainfall of about 2,400 mm (FITZGERALD et al. 2002).

Atelopus hoogmoedi males are commonly encountered along streams in the area during visits by the first author in 2003 and 2004 (LUGER et al. 2008). We studied a population

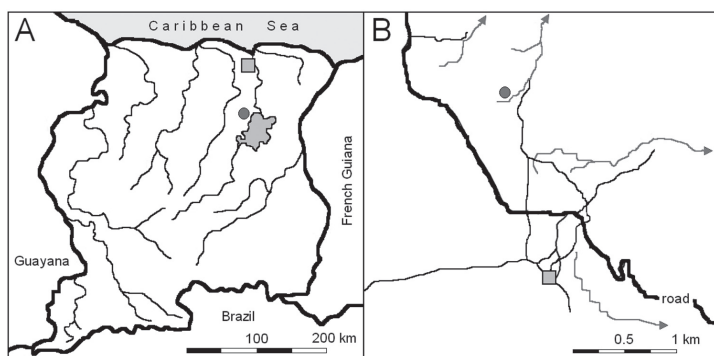


Fig. 1. (A) Suriname with major river systems (thin black lines), Van Blommenstein Meer (grey), Paramaribo (square) and location of Brownsberg Nature Park (circle). (B) Aspect of Brownsberg Nature Park with main road (bold black line) and tracks (thin black lines), headquarter (square) and creeks (thin grey lines with arrows); the location of the 1000 m² study area along the Koemboe creek where *Atelopus hoogmoedi* was studied is indicated by a circle.

of *A. hoogmoedi* from 19 April to 18 August 2004 (47 observation days) along Koemboe creek (Fig. 1). This small stream, bordered with riparian forest, is located approximately 2 km from the main research station of the park (4°56'39.8" N, 55°11'47.7" W; ca. 370 m above sea level). The streambed is 3 m wide on average; water depth varies between 10 and 80 cm. The stream gradient results in numerous small cascades with splash zones and pools below. Stream banks consist of sand, gravel and large boulders. Several fallen trees are found alongside and across the stream. The vegetation bordering the stream margin was mainly composed of *Heliconia* sp. and other herbaceous plants such as ferns and palms. Mean air temperature during the study period (taken every two hours day and night with four Gemini data loggers) was 23.0 ± 0.96 °C (range 20.8–27.6 °C; $n = 1,500$); total precipitation was 1,250 mm (measured continuously with an automatic rain gauge).

Based on the first author's preliminary observations on *A. hoogmoedi* at the study site, a 1000 m² plot (25 × 40 m, with the 40 m border parallel to the stream) was established to facilitate observations. It was divided into a 5 m × 5 m grid system, which covered both stream banks and the forested hill north of the stream. Every second to fourth

day, from 06:30–18:00 hrs, the entire plot was surveyed for toads (i.e. in leaf litter, on fallen tree trunks, rocks and vegetation up to 2 m above ground). Each of the 19 male individuals encountered was weighed with a digital mini scale (Kwang HWA e68–50, readability 0.01 g) and measured (snout-urostyle length, SUL) to nearest 0.1 mm using a calliper when collected for the first time. Mean weight was 1.4 ± 0.2 g (range 1.1–1.9 g); mean SUL was 26.1 ± 1.3 mm (range 24.1–28.9 mm).

For mark-recapture purposes, the dorsal and ventral pattern of every specimen was photographed with a Fuji digital camera when encountered. Since colour patterns in this species are constant and differ remarkably among individuals, individual recognition was possible through comparison of photographs. Capture locations were marked with labelled flags to estimate home range. The position within the plot was taken with a measuring tape relative to the grid system. In addition, substrate type (leaf litter, low vegetation, rocks, logs, trees) and height above the ground were recorded for every capture event.

To determine the relationship between (1) the distribution of capture locations and habitat structures as well as between (2) the distribution and size of home ranges and en-

vironment, habitat structures occupied by male *A. hoogmoedi* were quantified for each 5 m × 5 m square by counting individual structures, i.e. density of understory growth (including herbaceous plants and palms ≥ 50 cm in height and trees ≤ 3 cm diameter at breast height), trees (> 3 cm diameter at breast height), fallen tree logs (≥ 10 cm in diameter) and rocks (≥ 50 cm in diameter). In addition, the slope was quantified. We chose these parameters based on observations made by the first author at the same study during an earlier visit.

Data analysis

Site fidelity was evaluated with a recapture decay plot in the manner described by BROWN & EHRLICH (1980). From the slope of the regression line in the linear area ($y = 1.306 - 0.012 x$, whereas: $x = \text{natural log of the number of individuals in residence} \times \text{days}$), we calculated the mean residence rate during the study period as e^m , $m = -0.012$ (see WARREN 1992). This residence rate is an estimate of the percentage of individuals recorded on one day that stay in the area until the next observation.

Home ranges were calculated as fixed kernels (Animal Movement 2.0 extension for the ESRI GIS software ArcView; HOOGE & EICHENLAUB 1997). The kernel approach is a contouring method that calculates different probabilities of presence for any point within the home range of an individual (see WORTON 1989, SEAMAN & POWELL 1996). The contour smoothing factor h was estimated individually from the data set obtained in the field, according to the least square cross validation method, LSCV (e.g. RODGERS & CARR 1998; <http://blue.lakeheadu.ca/hre>). Home ranges were computed for eight individuals (with ≥ 10 recaptures per individual) with the Animal Movement 2.0 extension for ArcView. Outliers (maximum 5% of original observation points) were removed by the implemented function Outlier Removal according to the harmonic mean method (DIXON &

CHAPMAN 1980). With this method points can be removed by their largest harmonic mean value. Home range size ($n = 8$) was correlated with an index of body condition of the toads using a Spearman rank correlation. The index of body condition was calculated as: $\text{body weight}/\text{SUL}^b \times 10^{-3}$ with $b = \lg[\text{body weight}]/\lg[\text{SUL}]$ (see HEMMER & KADEL 1972).

Habitat utilization: We wanted to determine if correlations existed between (i) capture locations and physiographic habitat parameters, as well as between (ii) distribution of home ranges (presence/absence) and physiographic habitat parameters. Therefore, we quantified habitat structures, including density and position relative to the stream of understory growth, trees, dead wood and rocks. We performed two principal components analyses on (1) habitat structure data from 5 m × 5 m squares occupied by *Atelopus hoogmoedi* and (2) on habitat data from all squares, whether occupied or unoccupied. We used a multiple linear regression analysis (stepwise forward) to examine which factors determined the distribution of occupied locations, using data only from squares in which toads were found. Using logistic regression, we determined which habitat characteristics differentiated occupied from unoccupied sites. All statistical analyses were performed with Statistica (StatSoft).

Results

Site fidelity

During our study, we in total encountered 19 male individuals within the 1000 m² plot. Three of them were observed only once and two were recaptured only once. The remaining 14 were recaptured more than one time. Along the studied stream, the relative abundance of male toads was 0.475 per meter. According to the recapture decay plot, male *Atelopus hoogmoedi* showed strong site fidelity along the stream (Fig. 2). The low decline of the number of recaptures in the first few days

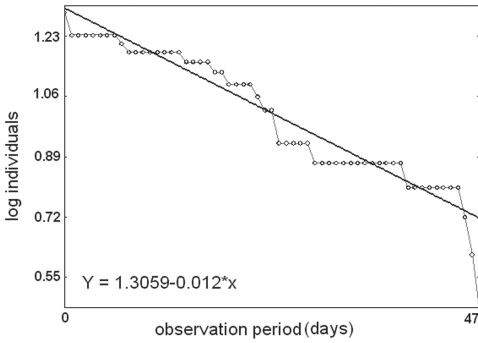


Fig. 2. Recapture decay plot for 19 *Atelopus hoogmoedi* males between 19 April and 18 August 2004.

of observation indicates little migration or mortality during the study period. Furthermore, the high residence rate (0.988) suggests strong site fidelity.

Home ranges

Among the eight males for which home ranges could be computed (see Fig. 3) the mean size of the 95% utilization probability area (UPA) was $38.1 \pm 17.7 \text{ m}^2$ (range 6.4–60.7 m^2). The 95% UPA showed overlap to some extent among some individuals (Fig. 3), whereas the activity centres (50% UPA, mean size $5.4 \pm 3.4 \text{ m}^2$; range 1.2–10.6 m^2) almost did not overlap (Fig. 3). Spearman rank correlation revealed a significant negative correlation between home range size and body condition (95% UPA: $R = -0.762$, $p = 0.028$; 50% UPA: $R = -0.786$, $p = 0.021$; mean index of body condition 1.03 ± 0.1). There was no correlation between residence time of individuals and the sizes of the home ranges.

Habitat utilization

Home range (Fig. 3) and capture locations (not shown) were non-randomly distributed. The two factor analyses reduced the six original correlated habitat variables to two un-

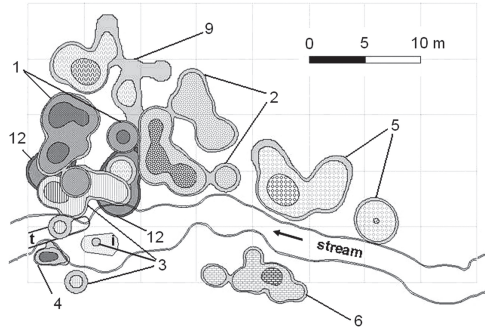


Fig. 3. Home ranges of eight male *Atelopus hoogmoedi* (numbered) calculated as fixed kernels within study plot (grid). Different isopleths border regions of equal utilization probability, i.e. the 95, 90 and 50% volume contours. Legend: t = fallen tree, i = island.

correlated factors. Concerning factor 1 both analyses revealed significant factor loadings for the variables ‘slope’, ‘distance to the stream’ and ‘density of understory growth’. With regard to factor 2 this was the variable ‘trees’. Regarding the factors which determined (i) the distribution of the capture locations, we found that they were only explained by factor 1 (Beta = 0.434 ± 0.167 , $p = 0.015$; Fig. 4). According to the logistic regression model (Fig.

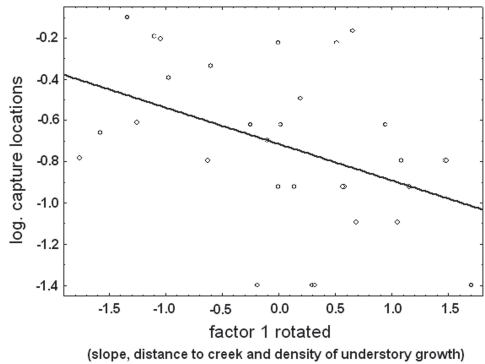


Fig. 4. Multiple linear regression: correlation between capture locations (between 19 April and 18 August 2004 in a 1000 m^2 study area; see Fig. 1) and factor 1 (Beta = 0.434 ± 0.167 , $p = 0.015$), determining the distribution of capture locations; significant factor loadings were obtained for the variables slope, distance to stream and density of understory growth.

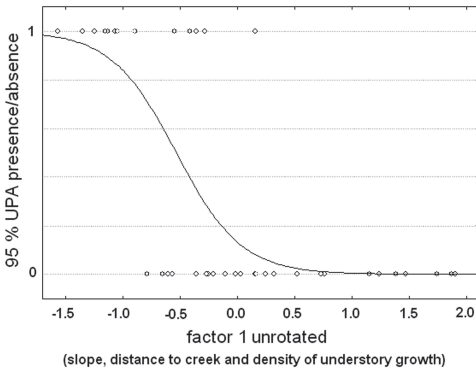


Fig. 5. Logistic regression: correlation between presence/absence of home ranges (95% UPA) of eight *Atelopus hoogmoedi* (between 19 April and 18 August 2004) and factor 1 (significant factor loadings obtained for variables slope, distance to stream and density of understory growth); distribution of home ranges was determined by factor 1 ($\chi^2 = 25.55$, $p < 0.001$, estimated parameter = -3.754 ± 1.297 , $t(37) = -2.895$, $p = 0.006$). One outlier ($x = 2.19$; $y = 1$) was removed prior to statistical analysis.

5, Maximum Likelihood, $n = 39$ squares, one outlier removed before statistical analysis), presence of home ranges (ii) again were determined by factor 1 ($\chi^2 = 25.55$, $p < 0.001$, estimated parameter = -3.754 ± 1.297 , $t(37) = -2.895$, $p = 0.006$). Males were found between 0 and 173 cm above the ground (mean 51.95 ± 36.7 cm, $n = 226$) in low vegetation (48% of all encounters), on trees (6%), on rocks (17%) and tree logs (15%). Only 14% of the observations were made in leaf litter.

Discussion

Male *Atelopus hoogmoedi* showed strong site fidelity during our study period. Capture locations showed a clustered distribution. Males maintained activity areas in locations covered with dense understory vegetation near the stream for up to four months. We found a significant negative correlation between home range size and body condition. Specimens were frequently observed at ele-

vated spots up to 1.73 m above the ground in low vegetation (48% of the encounters).

Site fidelity and the maintenance of a defined home range are considered advantageous since knowledge of the environment favours orientation and therefore make feeding more efficient; escape routes and shelter are easier to find (WELLS 2007). In our study species, we expect that an additional reason may play a role. Male mate choice is well known in *Atelopus* (e.g. LÖTTERS 1996), as males try to get into amplexus with conspecific females by clasping almost anything that appears suitable. Females commonly appear at the breeding sites (streams) only for purposes of reproduction. For these reasons, it might be reasonable for a male to occupy a defined home range next to a stream well before females arrive. Interestingly, since our observations were made outside the breeding season (i.e. over the long rainy season), we conclude that mate choice may not be the only reason for maintaining home ranges.

Noteworthy, it could be costly to maintain a large home range as evidenced by the negative correlation between sizes of home ranges and body conditions of toads.

Maintenance of a home range during the rainy season in the proximity of running water may, in some instances, even be disadvantageous. Sudden floods, especially in canyons like in the study area, can wash away *Atelopus* populations (DUELLMAN & TRUEB 1986). Hence, a greater perching height may be preferred as a mechanism to avoid this. It should also allow for an increased chance to visually locate approaching females during the mating season and to attract them by calling activity. The fact that activity centres of home ranges (50% UPA) almost did not overlap indicates that *A. hoogmoedi* males show territoriality, although aggressive behaviour among males, as known in other *Atelopus* species (CRUMP 1988, LÖTTERS 1996) was not noticed at all during our study. Perhaps, active home range defence in *A. hoogmoedi* plays a minor role (different to home range maintenance) outside the breeding season.

Our observations on site fidelity, home range sizes and patterns and habitat utilization in *Atelopus hoogmoedi* as well as the apparent temporal and spatial segregation of males (and, by implication, of females) may be important for both in situ (e.g. monitoring, population census) and ex situ (captive breeding) conservation programs. Ex situ breeding success of *A. hoogmoedi* at the Atlanta Botanical Garden increased after temporal separation of the sexes prior to mating (R. GAGLIARDO, pers. comm.). This coincides well with our findings. We recommend simulating conditions of the rainy season when keeping males separated from females. Due to the fact that males occupy home ranges at the reproductive site and that this may play a role in mate choice, reproductive success in captivity may be higher when females are moved to males in containers that have running water for egg deposition. Low male density and home range size in the wild should be considered when populating tanks with males. Besides from running water, tanks should allow toads to climb perching sites, because in the wild, males were mostly found on low vegetation.

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