

Site fidelity and patterns of short- and long-term movement in the brilliant-thighed poison frog *Allobates femoralis* (Aromobatidae)

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Abstract We studied movement and site fidelity of males and females of the territorial frog *Allobates femoralis* (Aromobatidae) in a population in the Nature Reserve “Les Nouragues” in French Guiana, South America. Observations during 3 months in 2006 ascertained intra-seasonal site fidelity for males and females. Males actively defend large multi-purpose territories whereas females retreat to small resting sites from where they commute to neighbouring males for courtship and mating. Female short-term movement corroborates the previous assumption of a polygynous or promiscuous resource-defence mating system. Year-to-year recaptures from 2005 until 2008 revealed distinct patterns of inter-annual movement for males and regional site fidelity for females. Males abandon their territories and have to re-negotiate them when reproduction starts again at the end of the dry season. Females are not subject to intra- or inter-sexual territorial competition and as a result move significantly less between reproductive seasons than males. Male long-term movement reflects spatial structure and prevailing social interactions and is a reliable indicator for tadpole deposition sites. The combined effects of intra- and inter-seasonal movement promote the diversity of mates for both sexes.

Keywords Dispersal · Site fidelity · Territoriality · Amphibia · Dendrobatoidea · Movement

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Introduction

The decisions of an individual to maintain or abandon centres of activity, as well as the causes for and consequences of these decisions, are pivotal points in the life history of a given species. Various hypotheses and theoretical models on the subject have been proposed, mainly in an ornithological context (Greenwood and Harvey 1982; Switzer 1993; Pasinelli et al. 2007 and citations therein for overviews). Surprisingly, given the extensive work on anuran social behaviour (Wells 1977, 2007; Sullivan and Heatwole 1995 for general summaries; Weygold 1987; Summers et al. 1999; Pröhl 2005 for dendrobatids), not all aspects of site fidelity in frogs have received equal attention. Current research is focused mainly on fidelity to spawning sites in pond breeding species (Sinsch 1988; Miaud et al. 2000; Pope and Matthews 2001; Sztatecsny and Schabetsberger 2005; Forester et al. 2006; Pellet et al. 2006) and to some extent on short-term site tenacity and homing ability (McVey et al. 1981; Crump 1986; van Wijngaarden and van Gool 1994; Chiu and Kam 2006). Beside in dendrobatids (Pröhl 2005), studies dealing with territorial behaviour and movement of hyper-dispersed anuran species were conducted in the families Bufonidae (Dole and Durant 1974; Crump 1988; Luger 2006) and Mantellidae (Andreone 1998; Heying 2001; Vieites et al. 2005). Additionally, various other aspects of movement in anurans, such as dispersal of post-metamorphs (Sinsch 1997; Patrick et al. 2007), individual movement (Ursprung et al. 2009) and orientation (Ferguson et al. 1968; Taylor and Ferguson 1970; Forester and Wisnieski 1991; Sjögren-Gulve 1998; Orgutsov 2004), were treated in previous studies. To our knowledge, no mark-recapture study of long-term site fidelity and year-to-year movement in prolonged breeding

and territorial anurans, especially Dendrobatoidea, has been conducted so far.

Previous work on the pan-Amazonian (Amézquita et al. 2006; but see Simões et al. 2008) arboreal frog *Allobates femoralis* demonstrated prolonged site fidelity of territorial males during the breeding season (Roithmair 1992; Magaña Mendoza 2008). Territories are advertised with calls that allow for intra- and inter-specific recognition (Gasser et al. 2009; Göd et al. 2007) and residents react aggressively to vocally active intruders (Narins et al. 2003, 2005; Hödl et al. 2004). Calling lasts throughout the reproductive season, which coincides with the rainy season (Gascon 1991), when males reduce or cease territory advertisement only during periods with little or no precipitation (Gottsberger and Gruber 2004). In French Guiana, a marked interruption of territorial and reproductive behaviour (Born and Gaucher 2001) occurs during the pronounced dry season from August to November (Grimaldi and Riéra 2001). After hatching at the terrestrial oviposition site, tadpoles have to be carried to terrestrial bodies of water, where they take 40–50 days until metamorphosis (Weygold 1980). Larval transport is usually accomplished by males (Lescure 1976; Aichinger 1991; Roithmair 1992). However, anecdotal reports of females carrying tadpoles exist (Silverstone 1976).

In *A. femoralis*, all reproduction-related behaviour takes place in the territory of the male, with the exception of tadpole development. Terrestrial bodies of water that are large and deep enough to persist until metamorphosis do not abound in the habitat of *A. femoralis* and in general are seldom found directly in, or close to male territories. Thus, tadpole development sites constitute an extraterritorial reproductive resource for *A. femoralis* males and can be expected to put constraints on male spatial behaviour. Furthermore, these bodies of water constitute well-defined population sources, as all juveniles initially have to disperse from the places of larval development. Consequently, the orientation of tadpole deposition sites to male territories can be expected to introduce directionality in an otherwise homogenous non-directional spatial setup. In this study, we make use of a natural simple spatial setup, where the only persistent body of water consists of a floodplain that parallels the study plot, to confine this directionality to a single axis, which facilitates further analyses.

In the behavioural literature, there exists a variety of theories on reasons for site fidelity, originating predominantly from avian research. In the discussion, we address three prominent hypotheses, namely the “reproductive performance hypothesis” (Switzer 1997), the “social constraints hypothesis” (Payne and Payne 1993) and the “site choice hypothesis” (Switzer 1997; Pasinelli et al. 2007) and speculate about their validity and potential for application in the case of our study species.

Materials and methods

Study site

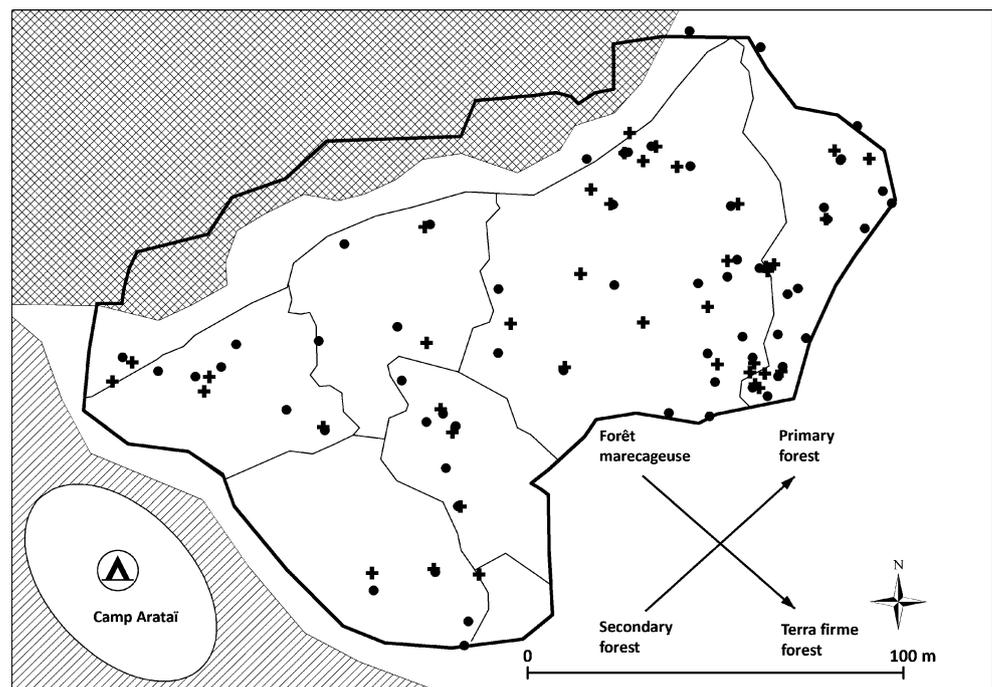
The study was conducted in tropical lowland wet rainforest (23 m a.s.l.) near the field station “Aratai” (3°59' N, 52°35' W; WGS84) on the river Arataye within the nature reserve “Les Nouragues”, French Guiana. The study population of *A. femoralis* is located in a forest (500 trees/ha, DBH >10 cm and 250 palms/ha) that is characterised by two gradients on a scale of several kilometres, well beyond the extension of the study plot. Lower areas are covered by regularly but not permanently flooded swamp forest (“forêt marecageuse”, fr.) which changes from NW to SE to non-flooded forest (“terra firme”, pt.; Poncy et al. 2001). A second transition occurs from old secondary forest near the riverbank (SW) to primary forest in the interior (NE). The plot of 20,095 m² is bordered by the forest edge near the camp (SW) and a flooded area with a shoreline, running at an angle of approximately 60° from north, forming during the rainy season (NW). Tadpoles of *A. femoralis* were regularly found inside this pool and it is the only permanent body of water within at least 500 m from our study area (Born and Gaucher 2001; Gottsberger and Gruber 2004). Initially, the extension of the plot to NE and SE was chosen in 2005 to comprise the territories of approximately 50 calling males (Fig. 1). In this year, no additional males were found within at least 30 m from the study plot. 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).

Monitoring

Monitoring took place during the following periods: January 16–24 in 2005 (9 days), February 6–April 27 in 2006 (81 days), February 6–11 in 2007 (6 days) and on March 4 and April 24 in 2008 (2 days). The study plot was scanned daily and every individual encountered was registered. All observation periods fell into the reproductive season of *A. femoralis* in French Guiana, lasting over the whole rainy season from the end of November until July (Gascon 1991; Gottsberger and Gruber 2004). From 2006 to 2008, an additional boundary zone of 30 m around the plot was included to detect movement beyond the border of the study plot.

In all years, we attempted total sampling of calling males by marking the calling positions of all sampled individuals and actively approaching callers in previously unsampled locations. An equal sampling effort was spent per unit area per year; however, the different behaviours of males and females resulted in different detection probabilities for either sex. Sampling in 2005, 2007 and 2008 was stopped, when apparently no new males were found. Only data from

Fig. 1 Outline of the study area with trails (*thin lines*) and its natural boundaries, the flooded area (*cross-hatched*) and the forest edge (*hatched*); centres of activity of males and females in 2006 are marked as *circles* and *crosses*, respectively; *arrows* indicate transitions of the vegetation on a larger scale



February 6–April 27, 2006 (81 days) were used to investigate intra-seasonal behaviour. In this year, 45 males (83%) were encountered within the first 9 days inside the study plot and no new males were found after 30 days of sampling. Considering the fluctuating nature of amphibian populations (Marsh 2001), the total individual counts and the number of recaptures from year to year (cf. Table 1) indicate that comparable proportions of the total population were sampled in each year.

Detection, capture and individual identification

Males were located acoustically at their calling sites. During times without calling activity, vocal responses were elicited by playing synthetic advertisement calls (SPL <75 dB at a distance of 5 m; Hödl 1983) using a CD player with a battery powered loudspeaker. Females were detected usually when their presence was revealed by courtship calls (Weygold 1980; Hödl 1983) from a nearby male. A few additional individuals were detected by chance when they were disturbed in the leaf litter during regular

monitoring. Vocally active males were attracted by broadcasting synthetic advertisement calls (SPL >75 dB at a distance of 5 m; Hödl 1983; Ursprung et al. 2009) towards the focal male from random directions between 1° and 360°. The speaker was initially set up at approximately 5 m from the calling male and then successively removed upon approach until no further phonotaxis was observed (Magaña Mendoza 2008). Data from these playback trials will be used in further studies to define “playback territories” by integrating the distances an individual is willing to leave its calling position during a playback trial to chase away the potential intruder. However, the data from these trials were not used in the present study. Finally, all individuals were captured with medium-sized transparent Ziploc® plastic bags.

We took digital images of the ventral patterns for individual recognition with the frogs inside the bag. Individual identification was done later by comparison of ventral patterns (Donnelly et al. 1994) using the image viewing software ACDSSee Pro™. Prior to release at the site of first detection, all individuals were weighted to the

Table 1 Yearly total captures of males and females and recaptures thereof

Year	Total m	Total f	1-year m recaptures	1-year f recaptures	2-year m recaptures	2-year f recaptures
2005	41	7	–	–	–	–
2006	94	49	11	2	–	–
2007	106	32	11	6	–	–
2008	33	4	6	1	2	1

m males, *f* females

nearest 0.1 g and measured to the nearest 0.05 mm with callipers. All individual-related data were recorded as feature attributes in ArcPad™ at the point of first detection, the endpoint of the playback trial and at additional locations if the approach deviated considerably (beyond the twofold standard deviations) from a direct approach as described by Ursprung et al. (2009).

Cartography

Spatial information was recorded on a pocket computer (Hewlett Packard iPaq™ hx4700) using the mobile GIS software ESRI ArcPad™ 7.0. A north–south/west–east 5-m grid of reference points was deployed for triangulation of all further positions, using binoculars with an integrated digital compass, rangefinder and inclinometer (Leica VEKTOR™). Mapped objects included living and dead trees (DBH ≥ 10 cm), palms, fallen logs and larger branches, trails and other structures (e.g. palm spatha and leaf) used as calling sites by male *A. femoralis*. Once sufficient objects were mapped by triangulation, positions of animals were assigned by drawing directly on the digital map. Field data were refined daily using ESRI ArcGIS™ 9.0 on a portable computer.

Spatial analysis

For all spatial analyses in this study, we exclusively used observed calling sites and other points of first detection. Locations obtained by playback trials, as described above, were omitted and will only be used in future studies. Autocorrelation of obtained locations was not eliminated by sub-sampling, following De Solla et al. (1999).

For intra-seasonal home-range analysis in 2006, we treated temporally consecutive observations of an individual as groups by applying inter-point cutoff distances of 10 m for males and 5 m for females, to account for territory or resting site shifts. The distances were arbitrarily chosen after a preliminary inspection of location data to enable resolution of serial territories or resting sites in the subsequent polygon analysis. Positions beyond 10/5 m and constituting either singular sallies or starting/end points of an observation series were excluded. In cases where two or more groups were separated by more than 10/5 m or interconnected only by a single observation, several serial territories or resting sites were assumed for an individual. The logically grouped observations were then used to calculate the extension of the home ranges or home-range parts with a modified minimum area (MMA) method (Harvey and Barbour 1965) as it was employed in previous studies on *A. femoralis* (Roithmair 1992). In this polygon method, only points within a distance of $\frac{1}{4}$ of the maximum distance between two locations of an individual (in this study, males 6.75 m,

females 3.3 m) are connected. Intra-seasonal site fidelity was considered, when at least three consecutive observations of an individual were made on separate days in its MMA home range. For distance analyses, we took the centroids of the MMA home ranges.

Previous studies (Roithmair 1992; Magaña Mendoza 2008; Gasser et al. 2009) and our own observations (this study) showed a high degree of site fidelity of male and female *A. femoralis* during the breeding season. Accordingly, any observation within the MMA home range of an individual can be supposed to be an equally accurate representation of its centre of activity. Due to too few recaptures of individuals in the other years, it would have been only possible to calculate true centres of activity for the long observation period in 2006. The data during the other years predominantly consisted of singular encounter positions for most individuals. To unify observations between years, we consequentially used the initial encounter positions of the individuals observed in 2006 instead of calculating true centres of activity, although the data would have permitted to do so.

Strict year-to-year site fidelity was defined by applying a cutoff distance of 10.5 m for males and 3.6 m for females. This corresponds to the maximum diameter of male territories and female resting sites when approximated as a circle, using MMA home-range sizes from 2006 (this study). However, given the characteristics of courtship and mating (Roithmair 1992, 1994; this study), female movement is linked to male territory size. To account for this, we applied the male cutoff distance to females to relax the criterion for female site fidelity in a second analysis.

Software and statistics

All position, distance and area measurements were obtained from the digital map and analysed in ArcGIS™ 9.0. For this GIS package, additional plug-ins were used: ET Geo Wizards (ET SpatialTechniques 2007), Hawth's Tools 3.26 (Beyer 2004) and XTools Pro 4.2.0 for ArcGIS (Data East 2003–2007). For data processing and statistics, we used Microsoft Excel™ 2007, Systat™ 10.2 and SigmaPlot™ 10.0. Directional statistics (Mardia and Jupp 2000) were calculated in Oriana™ 2.02e.

Normality of linear data was tested with the Kolmogorov–Smirnov test; the distribution of angular data was assessed with Rayleigh's uniformity test. The Kruskal–Wallis/Mann–Whitney *U* test and the Watson–Williams *F* test were used to test for significant differences in means of linear and angular data, respectively. For linear data, we used Pearson correlation, whilst correlations between linear and angular data were analysed with directional statistics (Mardia and Jupp 2000). The resulting linear–angular correlation coefficient is unsigned and does not give

information on the direction of a correlation. Therefore, we assessed internal structures of significant linear–angular correlations by comparing mean directions between three sub-samples. For this purpose, the observations were sorted and grouped equally by the corresponding linear values that were used in the preceding correlation analysis.

Results

Total counts and recaptures

Between 2005 and 2008, a total of 244 males and 82 females were identified in the study area and the surrounding boundary zone. Twenty-six individual males and nine females in the study area were recaptured inside the study area in the year following their initial detection, two of the males and one female also a second time 2 years later. Because the three individuals for which we had two recaptures showed different behaviour from one recapture to the other and between the sexes (cf. “year-to-year site fidelity”), we assumed that pseudo-replication did not occur in our data and retained the according observations. One of the recaptured males had moved from the boundary zone into the study area in the following year and was included in further analyses. Two additional males that were captured and recaptured exclusively in the boundary zone were not included in the analyses (Table 1).

Intra-seasonal behaviour

Territoriality and site fidelity

Of 54 males found inside the study area in 2006, 50 showed at least sequential site fidelity and territoriality. The criterion for site fidelity of three serial observations on separate days within the MMA home range was met within 3 to 60 days ($n=57$, $\tilde{x}=12$, $iqr=9$). Advertisement calls and phonotactic behaviour towards artificial advertisement calls were additional indicators of territorial behaviour. During 693 observations of males, three aggressive male–male encounters, where territory residents physically attacked an intruder who was moving and calling inside the territory, were registered. One individual did not establish a territory at all and moved erratically through the study area for at least 31 days. For three males with less than three observations, site fidelity could not be assessed. The 50 territorial males inhabited 57 territories during the observation period. Forty-four males occupied a single territory, five established two consecutive territories and one male shifted its territory twice. Territory occupancies were assured by three to 36 observations ($n=57$, $\tilde{x}=10$, $iqr=10$) of each territorial individual and lasted 5–79 days

($n=57$, $\tilde{x}=65$, $iqr=44$). Thirty-four males were still observed in their territories during the last week of our study. The extension of male territories or territory parts varied from 0.54 to 87.26 m² ($n=57$, $\tilde{x}=15.61$, $iqr=23.67$). As common in polygon methods, calculated territory size correlated significantly with number of observations ($r=0.643$, $p<0.001$) and duration of territory occupancy ($r=0.501$, $p<0.001$). However, when looking only at individuals with more than the median number of observations or more than the median number of days of territory occupancy, no significant correlation was found for number of observations ($r=-0.23$, $p=0.239$) nor for days of territory occupancy ($r=-0.234$, $p=0.231$) with the extension of the MMA territory. This indicates that the effect of an enlargement of MMA territories by increased sample size or duration of territory occupancy levels off before the median number of observations and the median number of days of territory occupancy in our study.

Of 37 females found inside the study area, 19 showed site fidelity whereas two individuals moved erratically. The criterion of three serial observations on separate days within the MMA home range was met within 3 to 44 days ($n=21$, $\tilde{x}=9$, $iqr=15$). For 16 females with less than three observations, site fidelity could not be assessed. Females did not exhibit territoriality and did not show any aggressive behaviour towards individuals of either sex. Two out of 19 females that exhibited site fidelity occupied two consecutive sites, all other were restricted to a single site. At these 21 sites, occupancies were assured by three to 23 observations ($n=21$, $\tilde{x}=4$, $iqr=3$) for each female and lasted 4–66 days ($n=21$, $\tilde{x}=20$, $iqr=29$). Fifteen females were still observed at their resting sites during the last week of our study. With an extension that varied from 0.006 to 10.08 m² ($n=21$, $\tilde{x}=1.10$, $iqr=5.83$), female resting sites were significantly smaller ($U=78$, $p<0.01$) than male territories. Extension of MMA resting sites did neither correlate significantly with number of observations ($r=0.3$, $p=0.187$) nor duration of site occupancy ($r=0.233$, $p=0.31$).

There was no significant correlation of distance to the waterline with neither the density of male territories ($r=-0.388$, $p=0.268$) nor the density of female resting sites ($r=-0.552$, $p=0.122$), although in both sexes, the density thinned out at the far end (Fig. 2). The extension of territories and resting sites did not correlate significantly with distance to the waterline for males ($r=-0.14$, $p=0.333$) and females ($r=0.352$, $p=0.139$), respectively.

Short-term movement

Observed male short-term movement consisted of territory shifts and sallies from territories. For six males occupying more than one territory, mean distance between consecutive territories was 24.1±7.49 m ($n=7$, range 12.76–32.45 m).

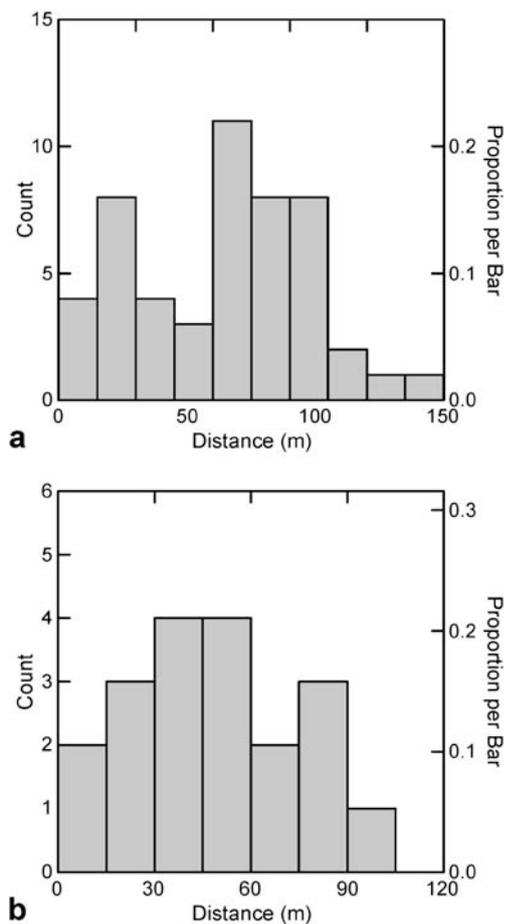


Fig. 2 Distances of the centroids of male (a) and female (b) MMA home ranges from the waterline

A single non-territorial male experienced a net displacement of 23.56 m with a straight path of 155.08 m between consecutive observations. One female inhabited two sites 19.09 m apart and two females that moved erratically experienced net displacements of 9.15 and 7.92 m whilst covering distances of at least 18.49 and 23.04 m, respectively, between consecutive sightings.

For males, we observed ten sallies of eight individuals with a mean net displacement of 21.7 ± 10.51 m ($n=10$, range 13.84–50.22 m). In females, we observed 25 sallies of 13 individuals that temporarily left their site for a mean distance of 12.21 ± 5.14 m ($n=25$, range 5.24–23.48 m). All but one sally were visits to neighbouring male territories where the females were found in the immediate vicinity (<1 m) of the courting resident male.

Inter-annual behaviour

Year-to-year site fidelity

In 28% ($n=28$) of the male and in 10% ($n=10$) of the female recaptures, the individuals exhibited strict site

fidelity from year to year. However, when applying the relaxed criterion for site fidelity in females, only 20% of them were found beyond the cutoff distance of 10.5 m. Of two males and one female that were recaptured twice, in 2007 and 2008, both males showed site fidelity from 2006 to 2007, whilst the female moved beyond the cutoff distance from 2006 to 2007 and 2007 to 2008. From 2007 to 2008, one of these males left his former territory. The second male moved further (11.53 m) than the cutoff distance from 2007 to 2008, but as it ended up as close as 6 m to its initial detection in 2006, we assumed site fidelity as well. All cases with strict site fidelity were excluded from further analyses of year-to-year movement, as they have to be interpreted as stochastic motion within an individual's home range and not as "true" year-to-year displacement.

Year-to-year movement

Male (m) and female (f) displacement between 2005–2006 ($n_m=11$, $n_f=2$), 2006–2007 ($n_m=5$, $n_f=5$) and 2007–2008 ($n_m=6$, $n_f=2$; Fig. 3) did not differ significantly in length (males: $H=2.643$, $p=0.267$; females: $H=2.333$, $p=0.311$) nor in direction (males: $F=0.955$, $p=0.402$; females: $F=0.247$, $p=0.789$) between observation periods. Hence, we pooled all year-to-year observations for males and females, for further analyses. Male median net displacement between years was 28.42 m ($n=22$, range 14.09–101.37 m, $iqr=21.65$) whereas for females, it was 7.17 m ($n=9$, range 4.71–23.29 m, $iqr=5.93$), resulting in a significant difference between the sexes ($U=8$, $p<0.01$; Fig. 4). The mean bearing of annual displacement was $101 \pm 75^\circ$ (circular standard deviation, CSD) for males and $23 \pm 92^\circ$ (CSD) for females. However, Rayleigh's uniformity test revealed that only male annual displacement showed a significant preferred direction ($Z=4.05$, $p=0.016$) whereas female displacement was uniformly distributed ($Z=0.692$, $p=0.514$; Fig. 5).

A significant correlation existed between the initial distance of an individual male to the nearest permanent body of water and the direction of its displacement until the next year ($r=0.614$, $p<0.001$). Likewise, a male's initial distance to the forest edge and the direction of its displacement until the next year were correlated significantly ($r=0.431$, $p=0.028$). The mean angle of displacement changed from $123 \pm 55^\circ$ (CSD; $Z=3.151$, $p=0.037$) over $131 \pm 50^\circ$ (CSD; $Z=3.309$, $p=0.03$) to $19 \pm 55^\circ$ (CSD; $Z=2.748$, $p=0.059$) when comparing the near ($n=8$), intermediate ($n=7$) and far ($n=7$) third of observed displacements in relation to the waterline (Fig. 6). The differences between the mean displacement angles of the three sub-samples were significant ($F=7.114$, $p=0.005$). When sorted by the distance to the forest edge, the mean

Fig. 3 Outline of the study area with inter-annual displacement vectors for males (circles at endpoint) and females (crosses) and the flooded area (cross-hatched) and the forest edge (hatched); box shows mean annual displacement for each sex

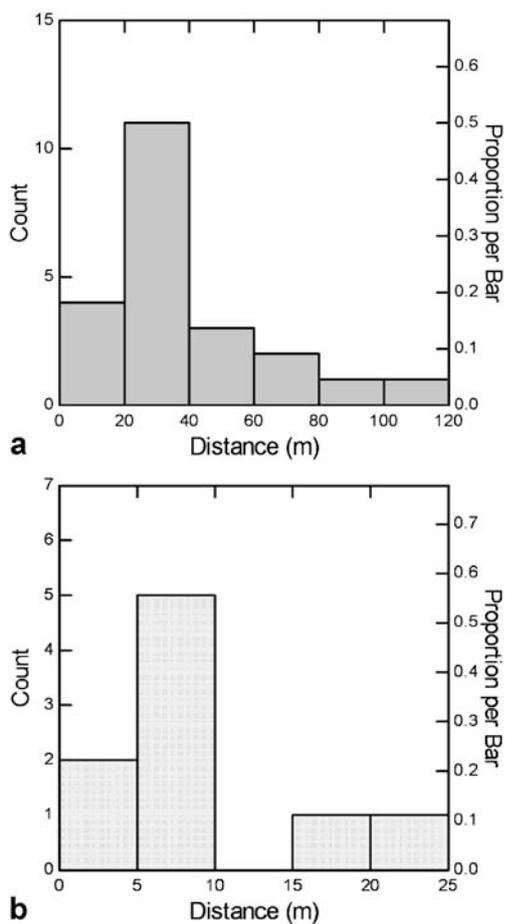
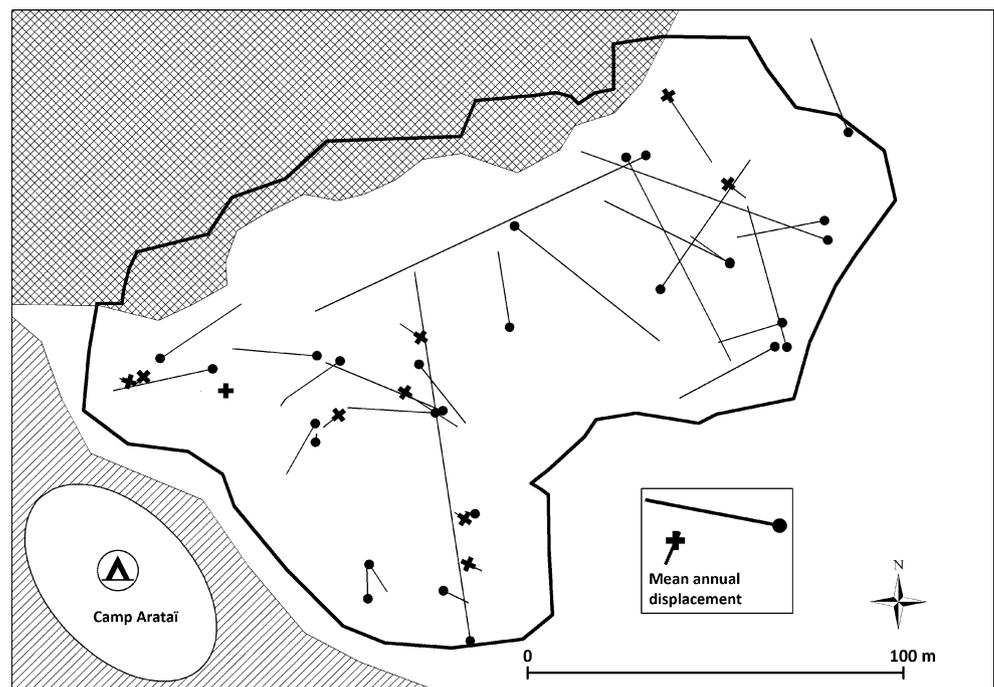


Fig. 4 Distances of male (a) and female (b) inter-annual displacement

angle of displacement changed from $70 \pm 67^\circ$ (CSD; $Z=1.998$, $p=0.136$) over $90 \pm 96^\circ$ (CSD; $Z=0.435$, $p=0.664$) to $130 \pm 48^\circ$ (CSD; $Z=3.438$, $p=0.026$) when comparing the near ($n=8$), intermediate ($n=7$) and far ($n=7$) third of observed displacements (Fig. 7). The differences between the mean displacement angles of the three sub-samples were not significant ($F=1.356$, $p=0.281$). For females, neither of the distances was correlated significantly with the angle of annual displacement (water: $r=0.622$, $p=0.095$; forest edge: $r=0.594$, $p=0.11$).

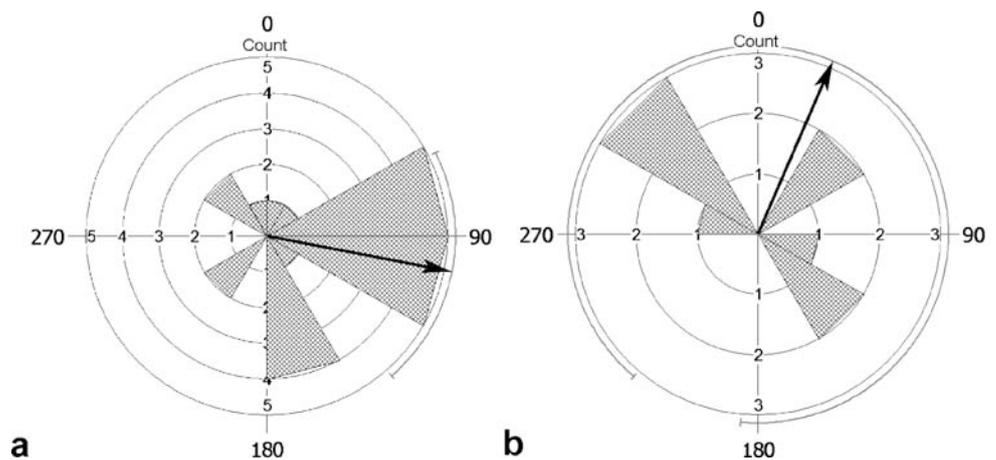
Additional observations

In 2006, we found 18 *A. femoralis* clutches inside the study area. Mean egg number per clutch was 15.5 eggs (range 3–24 eggs). Four males had more than one clutch (range 2–5 clutches) with a maximum of three clutches at the same time. All males that were observed guarding a clutch maintained their territory after the clutch was found empty. We were unable though to observe whether the tadpoles were transported or if the clutch was depredated. Seven males were observed during tadpole transport towards the floodplain and subsequently found back in their territory within several hours and not later than in the morning of the next day.

Discussion

Male and female *A. femoralis* show distinct patterns of space use and intra- and inter-seasonal movement that are

Fig. 5 Rose histograms of annual displacement directions for males (**a**) and females (**b**) with circular mean (*arrow*) and 95% confidence intervals (*outer line with peripheral whiskers*); frequency relative to radius, 30° classes



linked to different functions of territories in males and resting sites in females. Male inter-annual movement corresponds to the location of male territories in relation to tadpole deposition sites.

Territoriality and intra-seasonal site fidelity

Males

Territory sizes of male *A. femoralis* in Arataï differed strikingly from extensions reported in previous studies. Although the density of our study population (27 males/ha, 18 females/ha) was 14–18 times lower than of the population in Panguana, Peru (388–496 males/ha, 222–240 females/ha; Roithmair 1992, 1994), territory sizes did not scale with varying densities. Using the same estimation method (MMA), male territories in Arataï were only two to four times larger than in Panguana ($0.25\text{--}26.2\text{ m}^2$, $\bar{x} = 7.6$, $\text{iqr} = 11$). This aligns with findings in *Oophaga (=Dendrobates) pumilio* where no correlation of density and home-range size was found (Donnelly 1989a). The territories of male *A. femoralis* are “all purpose territories”, used for feeding, shelter, display and calling, courtship and oviposition. Previous studies

demonstrated that the resources related to these functions are usually not in short supply in tropical rainforests (Toft 1980; Donnelly 1989b; Lima and Magnusson 1998; Santos et al. 2004; Juncá and Eterovick 2007), the habitat of *A. femoralis*. Only territory size could be found to correlate with male reproductive success, thus constitutes a “resource” to be defended (Roithmair 1992). The observed self-induced limitation of territory size, albeit the vast surplus of available area, indicates an upper trade-off limit between benefits and costs of a large territory. We assume that between this upper limit and a minimal territory size that is necessary for feeding and shelter, actual male territory size is mainly determined by social and acoustic constraints. For other anurans, density of the population, calling intensity of individuals, availability and arrangement of calling sites and the density and structure of the surrounding vegetation have already been found as dominant factors for the spatial territory setup (Wells and Schwartz 1982; Robertson 1984; Wilczynski and Brenowitz 1988; Bosch and De la Riva 2004). This remains to be verified for *A. femoralis* in further studies.

Our observations in 2006 show strong male site fidelity throughout the breeding season, lasting up to 79 days and

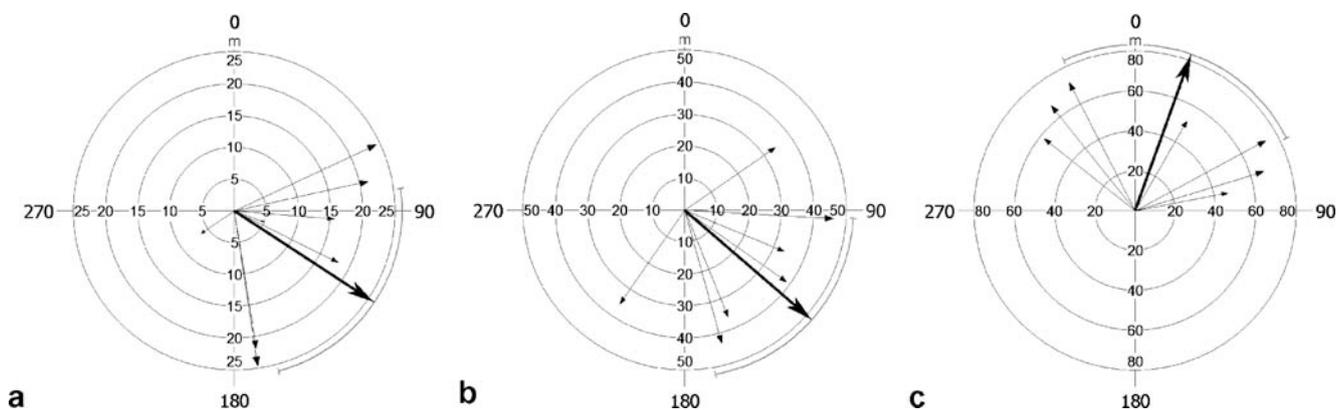


Fig. 6 Rose vector scatterplots of inter-annual displacement of males that were near (**a**), intermediate (**b**) and far (**c**) from the waterline with circular mean (*bold arrow*) and 95% confidence intervals (*outer line with peripheral whiskers*)

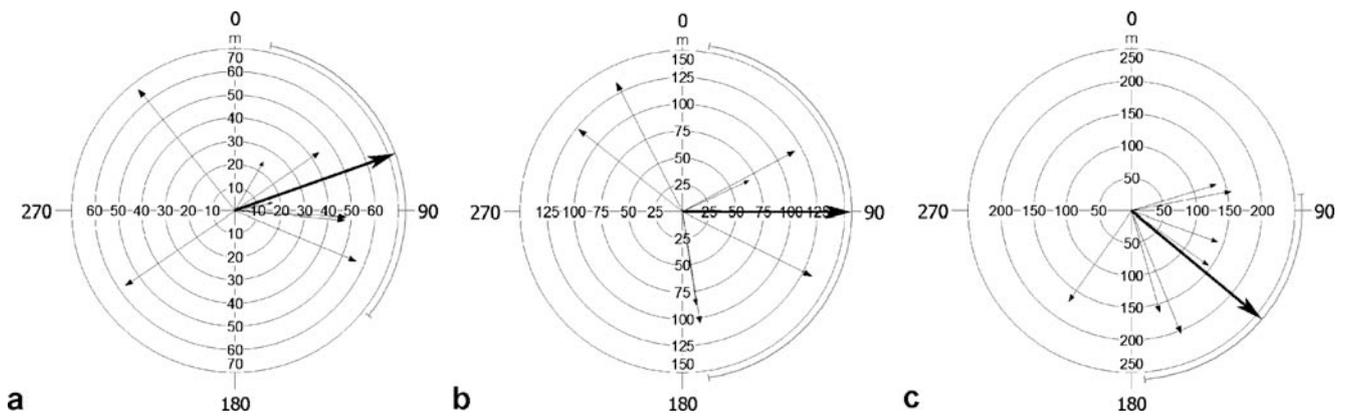


Fig. 7 Rose vector scatterplots of inter-annual displacement of males that were near (a), intermediate (b) and far (c) from the forest edge with circular mean (**bold arrow**) and 95% confidence intervals (*outer line with peripheral whiskers*)

probably far beyond, as most territorial males were still observed during the last week of our study. None of the reproducing males abandoned its territory in the course of our study. This indicates that intra-seasonal site fidelity is the usual condition in *A. femoralis* males and that they do not actively search for new or better territories during the breeding season. Homing behaviour in amphibians has been demonstrated in various species (McVey et al. 1981; Crump 1986; Diego-Rasilla et al. 2005; Chiu and Kam 2006) and is mediated by olfactory (Forester and Wisnieski 1991; Orgutsov 2004), magnetic (Diego-Rasilla et al. 2005), visual (Ferguson et al. 1968), celestial (Taylor and Ferguson 1970) and acoustic (Passmore and Telford 1981) cues. The latter cues are most likely to play a central role for the homing abilities of *A. femoralis*, as recent studies have shown that the properties of advertisement calls allow for the differentiation between individuals (Gasser et al. 2009) and thus can be used for long-distance orientation as well.

Females

Similar to their male conspecifics, female *A. femoralis* showed consistent site fidelity in 2006, lasting up to 66 days and probably beyond. This observation contradicts previous studies, where females were described as moving freely between potential mates (Roithmair 1992, 1994). Sampling males prior to mating and female multiple mating is expected under the assumption of a resource defence mating system (Arak 1983; Poelman and Dicke 2008) and the “good genes” hypothesis (Ihara 2002). Observations in captivity have shown that females are able to produce a clutch every 8 days (range 3–20 days; Weygold 1980; Hödl, unpublished) when sufficient food and suitable conditions are available. This provides them with ample time for movement between different males and repeated sampling between two ovulations. Indeed, we could

observe such sampling behaviour, but females homed back to defined resting sites, consisting of only a single root or branch, which they did not defend against conspecifics of either sex. Studies on *Oophaga (=Dendrobates) pumilio* revealed that differences in home-range sizes between the sexes are an indicator for different home-range functions (Donnelly 1989a; Haase and Pröhl 2002). In fact, in *A. femoralis*, all reproduction-related functions of a territory needed by a female, namely courtship area and egg deposition sites, are situated within male territories. The size of female resting sites thus constitutes the minimal area needed by an individual for only feeding and shelter. Given the properties and characteristics of the habitat (cf. section on male territoriality), equally good conditions can be found at a multitude of locations throughout the forest. Females could reduce locomotion costs and predation risk by always using the closest suitable site for resting and feeding. Therefore, it is highly unlikely that females show site fidelity only because of superior conditions for survival at the location of their resting sites. Consequentially, female intra-seasonal site fidelity has to be explained by the advantages to be familiar with the local habitat and the social environment (Switzer 1993). Valid information on surrounding males probably can only be obtained by prolonged eavesdropping on male interactions (Otter et al. 1999) to assess the quality of potential mates through their call properties (Doty and Welch 2001; Pröhl 2003; Forsman and Hagman 2006).

Inter-annual movement and site fidelity

Observed directionality of annual displacement in males has two components that are orthogonal to each other and normal to the forest edge and shoreline, respectively. A geometric edge effect and probably active edge avoidance (Bollinger and Switzer 2002) drives males towards the interior in the following year when they were located close

to the forest edge before. This effect diminishes for individuals further inside the forest. Inter-annual movement along the other axis is more complex. The initial perpendicular distance to the waterline and the angle of inter-annual displacement of recaptured males correlate significantly. Hence, males close to the floodplain in 1 year were found further away the next year, whereas males distant to the waterline tend to move closer. The linear–circular correlation turning counter-clockwise is a result of the first component that is running normal to the forest edge.

After tadpole transport, males reliably return to their territories and their whole spatial setup is highly static during the breeding season, giving no indication for any directed movement from year to year. However, there are directed processes between two reproductive seasons that help to explain inter-annual movement. During this time, juveniles emerge from their developmental sites and move into the adjacent forest. As long as they do not vocalise, they will not experience any aggression from territorial vocally active males (Roithmair 1992) and can move uninhibited in the area. Notwithstanding any probable phonotactic orientation of juveniles towards calling males, analogous to chorus orientation of adults in explosive breeding species (Bee 2007), juvenile dispersal is a diffusion process that originates from the developmental site. Accordingly, juvenile density has to be negatively correlated with distance to the source, which results in a density gradient. During the dry season, adult males cease territorial behaviour, as costs (Wells and Taigen 1986; Wells 2001) outbalance reproductive benefits. Nine months after emerging from their developmental sites, the oldest progeny of last season's territory holders reach sexual maturity (Weygold 1980; Hödl, personal observation). This coincides with the start of the rainy season and a new reproductive period, and the young males now compete for territories with survivors from preceding years. This competition leads to a directed expansion of all individuals that is driven by the juvenile density gradient. With increasing distance from the tadpole deposition site, this effect is counterbalanced by the requirement to minimise the risk of predation and territory loss that comes for breeding males with longer times needed for tadpole transport. Consequentially, males that were situated further away from the waterline in 1 year have the tendency to move closer until the next year and can do so, because due to their location, they are less affected by the juvenile density gradient.

Females, although they do not exhibit strict site fidelity, nevertheless are far less mobile between years than male *A. femoralis*. We interpret this regional fidelity to be a result of missing aggressive behaviour of females towards conspecifics of either sex. During the breeding season, females actively enhance their genetic mate diversity by sampling

and probably mating with several males that are arranged in a static setup. As males move significantly more from year to year than females, genetic mate diversity is enhanced further for surviving individuals of both sexes, as they are unlikely to end up with the same mating partners than the year before. Further research using molecular methods is needed, to investigate the details of the mating system in *A. femoralis*.

Theoretical context

Reproductive performance hypothesis

Individuals may use information on their own reproductive success to make decisions on migrational behaviour (Switzer 1997). Site fidelity should correlate with high former reproductive performance. Male *A. femoralis* can only evaluate their reproductive success in terms of clutches obtained and tadpoles transported. However, neither post-breeding dispersal nor active search for better territories was observed during the breeding season. Females return to their resting sites after mating and cannot obtain any further information regarding their own reproductive success beyond the production of the actual clutch (but see Silverstone (1976) for accounts on female tadpole transport). An extension of this hypothesis integrates the use of “public information” (Dall et al. 2005; Valone 2007) about reproductive success of conspecifics into decision making. However, it is very unlikely for either sex of *A. femoralis* to be able to assess the reproductive performance of conspecifics. Tadpole transport usually takes less than half a day (Roithmair 1992), giving hardly any information from ceased calling during that time as it will be superimposed by individual and temporal variation in calling activity. Information might be even obfuscated, like with the attenuated courtship call (Weygold 1980; Hödl 1983) that is adapted not to draw attention on reproductive activities of males.

Social constraints hypothesis

Due to competition, conspecific density beyond a critical threshold is expected to favour dispersal (Payne and Payne 1993). In general, this threshold can be either an absolute one or relative to some property of the distribution of individuals. In *A. femoralis* males, we believe the density threshold to be relative to the density at an equal distribution of all individuals, as the species is known to occur at much higher densities than the ones observed during our study. When this density is surpassed locally, this leads to migration, in our case, the directional year-to-year movement in response to a density gradient. Accordingly, females do not show this pattern due to lacking inter- and intra-sexual aggression during site choice.

Site choice hypothesis

Site fidelity can be expected when the probability to improve relative territory quality by dispersal is low. To allow successful territory shifts that improve the fitness of an individual, heterogeneity in mean within-territory quality and the ability to predict territory quality before movement are necessary (Switzer 1993; Pasinelli et al. 2007). If there are no differences between potential sites for territories or if an individual is unable to predict the quality of a new territory to some degree, it would not make sense in the beginning to initiate territory shifts. Previous studies demonstrated that there are significant differences in territory quality, namely territory size, that influence reproductive success (Roithmair 1992). However, it seems highly unlikely that *A. femoralis* is able to assess and predict the factors that are supposed to determine territory size (i.e. habitat acoustics, calling sites and social arrangement) and evaluate them against potential costs, prior to eventual dispersal. Thus, intra-seasonal site fidelity of *A. femoralis* is most likely to be caused by the lack of prognostic abilities regarding possible territories in the future and the accompanying risk of “losing it all” when endeavouring in active search for better territory locations during the breeding season.

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