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ABSTRACT

While spectacular large-scale movements of anuran amphibians like mass migrations and habitat invasion received a lot of attention, fine-scale spatial behavior remains largely understudied. This gap is especially surprising for species showing long-term site fidelity and thus display their whole behavioral repertoire on small ranges. Neotropical poison frogs (Dendrobatidae) are well known for their complex behavior and versatile reproduction and parental care strategies. Studying fine-scale movement with conservative capture-mark-recapture approaches is difficult in unobtrusive amphibians: frogs are hard to find, repeated captures affect their behavior and the number of data points is too low to allow a detailed interpretation of individual space use and time management. In this study, we overcome those limitations by equipping inconspicuous poison frogs with a tag to monitor their location every hour. Although the ecology of the promiscuous aromobatid frog *Allobates femoralis* (BOULENGER 1883) is well studied, little is known about the spatio-temporal behavior of the non-territorial females who don't engage in acoustic and visual displays. We tracked 17 female frogs for 6 to 17 days to provide the first precise analysis of spatio-temporal patterns of site fidelity in this promiscuous species. Females moved on average 1 m per hour, the fastest recorded movement of ~24 m per hour was related to a subsequent mating event. Traveled distances and activity patterns on days of courtship and mating differed considerably from days without reproduction. Frogs moved more on days with lower temperature and more precipitation, but mating seemed to be the main trigger for female movement. Estimated home ranges after 14 days varied from 24.8 m^2 to 285.2 m^2 and courtship and mating associated space use made up for ~ 30% of the home range. *A. femoralis* females spend ~ 62% of their time in mostly one, sometimes two or three smaller centers of use ranging from 2.5 to 66 m^2. During the tracking, we observed 21 courtship events and 19 ovipositions involving 12 tagged females. For seven females, we observed two consecutive mating events. The average time between two successive clutch depositions was eight days and the average clutch size was 17.4 eggs, confirming Weygolds' (1980) observations for captive *A. femoralis* for the first time in a natural habitat. Females did not adapt their time or space management to the mean density of males in their surroundings, didn't show wide-ranging exploratory behavior and didn't monitor their previous clutches. Our study demonstrates how tracking can be used to fill the knowledge gap about patterns of fine-scale spatial behavior in poison frogs.

1. INTRODUCTION

The decision to stay at the current spot or to move to other places is crucial for many aspects of an animal's life including foraging, territorial behavior, mating strategies and responses to predators (Swingland and Greenwood 1983; Brown and Orians 1970; Murray and Fuller 2000; Sinsch 2010, 2014; Newton, 2008; Wells, 2007). It is influenced by biotic and abiotic factors and depends on the animals ability to orient in space and time, motion capacity and intrinsic state (Nathan et al., 2008). To uncover which aspects tune an animal's spatial behavior, it is necessary to integrate its' paths across all relevant spatio-temporal scales: causes and patterns of daily movement (e.g. foraging) often differ significantly from seasonal (e.g. breeding migration) or lifetime movement (e.g. foraging, migration and dispersal).

Any type of movement is costly and bears substantial risks: increased energy expenditure, conspicuousness to predators and exposure to harsh climatic conditions favor the decision to stay (Bell, 2012; Dingle, 2014). Accordingly, animals move only when necessary, often showing temporary or long-lasting preference for known areas. The return of an animal to a previously occupied area is termed site fidelity and is widespread in the animal kingdom from mammals (e.g. Ramsay & Stirling, 1990; Rydell, 1989; Schaefer, Bergman, & Luttich, 2000), over birds (e.g. Greenwood, 1980; Newton, 2008), reptiles (e.g. Bock, Rand, & Burghardt, 1985; Mortimer & Portier, 1989), fish (Binder et al., 2016; Warner, 1988), amphibians (e.g. Sinsch 1990, 2010), insects (e.g. Alcock, 1983; Richardson, Giuggioli, Franks, & Sendova-Franks, 2017) to molluscs (e.g. Chelazzi, 1990; Lind, 1989) (for general reviews see Swingland & Greenwood 1983; Switzer, 1993). Animals may show fidelity to various types of sites e.g. the location of birth, a breeding area, a stopover during migration or a territory that is defended against intruders (Switzer, 1993).

Most information on spatial behavior and site fidelity comes from capture-mark recapture (CR) studies, where scientists rely on refinding marked individuals to estimate characteristics of spatial behavior. For example, the home range – defined as the area traversed by the animal during its normal activities of foraging, mating and caring for young (Burt, 1943) - or factors influencing space use are often investigated by CR approaches. However, the high spatio-temporal resolution needed to analyse complex fine-scale behavior, e.g. patterns of site fidelity, demands a frequency of relocations that can hardly be obtained with conventional CR methods. Due to those limitations, fine-scale movement of highly sedentary animals is understudied, although critical to determine factors influencing the decision to move (e.g. Pontoppidan &

Nachman, 2013) as well as spatial memory and navigational abilities (e.g. Nams, 2006; Pašukonis et al., 2016) or to develop mechanistic movement models (e.g. McClintock et al., 2012). To fill the knowledge gap of why, when and where to move, we need to follow the study subjects steadily for extended periods of time, e.g. by attaching a device that emits or reflects a signal. In this study, we use tracking to investigate fine-scale movement in an organism that displays complex spatial behavior and site fidelity at a fine-scale: a Neotropical poison frog (Anura, Dendrobatidae).

Anuran amphibians are among the most diverse vertebrate groups in terms of species and reproductive strategies, and they inhabit terrestrial and aquatic ecosystems from the tropics to the subarctis (AmphibiaWeb. 2019. <https://amphibiaweb.org>; Wells, 2007). A vast majority of studies on amphibian space use focuses on migratory behavior of temperate amphibians characteristic of the seasonal and lifetime spatio-temporal scale, e.g. the synchronized mass migration from winter habitats to breeding sites, return migrations of adults among different parts of the habitat or dispersal of juveniles (e.g. Sinsch et al. 2012; Heusser, 1968; Sztatecsny & Schabetsberger, 2005) (see Richards, Sinsch, & Alford 1994; Sinsch 2010, 2014 for reviews).

The focus of tracking studies on frogs inhabiting the temperate zone is especially surprising as the diversity of anurans peaks in the tropics. Warm climate and high humidity throughout the year allowed the evolution of a great variety of reproductive modes and concatenated parental care strategies. For example, while explosive breeding frogs rarely exhibit prolonged parental care, frogs need to shuttle their larvae from terrestrial clutches to aquatic deposition sites where they complete their development in species showing nonaquatic oviposition (Crump, 1974; Duellman & Trueb, 1986; Summers & Tumulty, 2014; Wells, 2007). The challenge of when and where and how to care for offspring requires sophisticated spatio-temporal strategies, turning poison frogs into ideal model organisms to study ecological aspects of movement and orientation (Pittman, Osbourn, & Semlitsch, 2014; Sinsch, 1990, 2010, 2014). Although parenting strategies in this group of frogs have attracted a considerable amount of research (Brown, Morales, & Summers, 2010; Brown, Morales, & Summers, 2008; Dugas et al., 2016; Poelman & Dicke, 2007; Ringler et al., 2015; Roland & O'Connell, 2015; Schulte & Summers, 2017; Summers & McKeon, 2004; Summers & Tumulty, 2014; Summers et al., 1999; Wells, 2007; Weygoldt, 1987), associated fine-scale movement patterns and factors affecting them have rarely been quantified and remain poorly understood.

Poison frogs are diurnal and mostly show long-term site fidelity or territoriality (Pröhl, 2005; Wells, 2007 for reviews), displaying their whole behavioral repertoire on relatively small ranges. Space use in this clade is shaped by various factors, e.g. parental care strategies (Brown, Morales, & Summers, 2009), parental state (Haase & Pröhl, 2002), number of surrounding mating partners (Folt, Donnelly, & Guyer 2018), distribution of reproductive sites (Donnelly 1989; Pröhl & Berke 2001) or abundance of food (Pough & Taigen, 1990). While male site fidelity in species with uniparental male care is closely linked to caretaking duties, the reasons for philopatry are less clear for the promiscuous females.

The Neotropic brilliant-thighed poison frog *Allobates femoralis* (BOULENGER 1883) (Dendrobatidae) is well-studied and perfectly suited to investigate fine-scale spatial behavior of promiscuous females: (1) they are large enough to fit transmitters for tracking (Pašukonis et al., 2014); (2) frogs can be identified by their unique ventral pattern, facilitating monitoring of individuals surrounding the focal frog (Ringler, Ursprung, & Hödl, 2009); (3) the high abundance and population density allows to obtain large sample sizes (Amézquita et al., 2009).

During the reproductive season, male frogs establish and defend territories which are advertised by calling from elevated structures such as palm leaves, logs or branches (Amézquita et al., 2006; Hödl, Amézquita, & Narins, 2004; Hödl, 1983; Narins, Hödl, & Grabul, 2003; Weygoldt, 1980). Female frogs are attracted by calling males and deposit clutches in the male's territory after a complex courtship (Montanarin, Kaefer, & Lima, 2011; Roithmair, 1994; Stückler et al., 2019; Weygoldt, 1980). The frogs' remarkable orientation skills (Pašukonis et al., 2017; Pašukonis et al., 2013) likely arise from transporting tadpoles from the leaf litter to water bodies, which is usually accomplished by male individuals (Lescure, 1976; Ringler et al., 2013; Weygoldt, 1987). Long- and short-term population monitoring with a CR approach has revealed many aspects of *A. femoralis* behavior and ecology (Ringler et al. 2009, 2013, 2014; Ursprung et al. 2011).

Tracking has been successfully applied to study spatial behavior and navigation in this species. For example, telemetry was used to quantify movements associated with tadpole transport (Beck et al. 2017; Pašukonis et al. 2017) or to demonstrate that *A. femoralis* males return to their home territory from several hundred meters after translocation (Pašukonis et al., 2014).

Female *A. femoralis* show seasonal and inter-annual site fidelity and seem to retreat to small 'resting sites' from where they commute to neighbouring males for courtship and mating (Ringler et al., 2009). Unlike the males, females don't defend territories or engage in acoustic

and visual displays. Hence, females are less conspicuous, harder to localize and more challenging to survey than calling territorial males. Accordingly, little is known about spatial and temporal movement pattern, time management and factors influencing motion in *A. femoralis* females. For example, it is unclear what size the female home range is and how it varies between individuals. We don't know how strictly they adhere to one location, whether they show ranging behavior to explore their surroundings, why, how far and how fast they move or if movement is influenced by weather conditions and density of mating partners. The aim of this study was to use tracking to fill the existing knowledge gap about fine-scale spatial behavior in female *A. femoralis* by addressing the following questions:

(1) What is the daily activity pattern of female brilliant-thighed poison frogs?
(2) Which factors influence female movement?
(3) What are the characteristics of female space use and how do they budget their time?

We integrate fine-scale data from tracking with seasonal CR based monitoring in *A. femoralis* and provide the first fine-scale spatial analysis of nonaggressive female site fidelity in promiscuous poison frogs.

Figure 1: Tag attachment. Female *A. femoralis* equipped with a miniature reflector tag for HDF telemetry, fixed to a waistband that is fitted to the size of the individual. Picture provided by A. Pašukonis.

2. MATERIAL & METHODS

2.1. Study species

The brilliant-thighed poison frog *Allobates femoralis* (BOULENGER 1883) is a small diurnal poison frog (Dendrobatidae: Aromobatinae; Pyron and Wiens 2011; AmphibiaWeb 2019; but see Grant et al. 2017 and Guillory et al. 2019) common throughout the Amazon Basin (Amézquita et al., 2009). Males establish and defend territories during the rainy season. They vocalize from leaf litter or slightly elevated structures to announce their area to male competitors and to attract females (Hödl et al., 2004). Females show non-aggressive site fidelity (Ringler et al., 2011) and deposit clutches of about 20 eggs in the male's territory after a complex courtship (Montanarin et al., 2011; Roithmair, 1994; Stückler et al., 2019; Weygoldt, 1980). Both sexes are polygamous and highly iteroparous but while females abandon the clutch shortly after oviposition (Ringler et al., 2013; Ringler et al., 2012; Ringler et al., 2009; Roithmair, 1992; Weygoldt, 1980). Males attend up to 6 clutches in their territory at the same time (Ursprung et al. 2011, Weinlein S., personal observation). After the initial larval development in the leaf litter for 15-20 days the tadpoles are transported to terrestrial waterbodies where the remaining development takes place (Weygoldt, 1980). Tadpole transport is primarily accomplished by male individuals (Ringler et al., 2013; Weygoldt, 1980), although females have been observed to flexibly compensate for male loss by taking over parental duties (Ringler et al. 2015).

2.2. Study site & study population

The study was conducted on a 4,6 ha river island located in the immediate vicinity of the CNRS research station 'Saut Pararé'(4°02'N/52°41'W), within the Nature Reserve ´Les Nouragues´ in a tropical rain forest in French Guiana. (Ringler, Mangione, & Ringler, 2015). The study area consists of primary terra-firme forest with seasonaly flooded areas on the edges of the island. This island in the Arataye River was originally not populated by our study species. The experimental population of *A. femoralis* was established in 2012, when 1800 tadpoles from the adjacent mainland population were introduced into artificial plastic pools on the river island. During the time of our study, the frogs primarily relied on an array of 13 artificial plastic pools (volume ~ 12 l, inter-pool distance ~ 20 m). A detailed high resolution map of the island was created using a north–south/west–east 5-m grid of reference points, including the exact position of living and dead trees (DBH ≥10 cm), palms, fallen logs, larger branches, trails, waterbodies and artificial pools (Ringler et al., 2014).

2.3. Data collection

2.3.1. **Monitoring**

Individuals were monitored during their reproductive season between 24. January and 14. April 2016 using a CR approach. For this purpose, we systematically surveyed the entire island to capture, map and identify as many frogs as possible. The procedure was repeated throughout the monitoring period with the attempt to sample the whole population and to gain information on the spatial distribution and stability of individual territory locations over time. The frogs were captured with transparent plastic bags, sexed by the presence (male) or absence (female) of the vocal sac and their unique ventral pattern was photographed for subsequent individual identification using the pattern matching software Wild-ID (Bolger, Morrison, Vance, Lee, & Farid, 2012). Spatial location, sex, current behaviour and picture number were carefully noted on a tablet PC (WinTab 9, Odys, Willich, Germany) using using a high-resolution map of the island in the mobile GIS software ArcPad 10.2 (ESRI, Redlands, CA, U.S.A.).

2.3.2. **Tracking**

Tracking of individual frogs was carried out between 8 February and 20 March 2016. Females were either tagged immediately after an observed clutch deposition or captured within the defined area by chance. We identified the frogs by their individual ventral pattern and fitted miniature transponders using a silicon-tube waistband with an additional strap between the hind legs to prevent the tag from rotating (Fig. 1). The reflector diode was color-coded, sealed with air-dry rubber (2 mm diameter) and connected to a T-shaped dipole antenna made of thin multi-strand coated beading wire. The long end (~ 12 cm) dragged freely behind the frog while the short end (~ 2 cm) was secured inside the waistband (as descibed in Beck et al., 2017; Pasukonis et al., 2013). We tracked the individual movement patterns of up to six individuals simultaneously between 6 and 17 days. For this purpose, we used a harmonic direction finder (RECCO R8, Recco AB) that emits a signal which is reflected by the tag on the waistband. We relocated the females every 60 minutes between 7.30 and 18.30 during their daylight activity period and recorded their position. We chose a lose fit for the waistbands to avoid egg binding, checked for eventual transponder-induced injuries every third morning and removed the tag if any wounds were visible. Because of the lose waistband fit, some females lost their tags. In most cases, we were able to find and retag the same individual and we further used the recaptures following a tag-loss event to check for injuries. Of the 17 tagged females, one was found dead after 6 days without any obvious predation event, one was found dead with a large spider in close proximity, two lost the tag and could not be recaptured to continue tracking, one

was de-tagged because of tag-induced injury of the skin, and one female disappeared without any trace. All other 11 females were purposely de-tagged after tracking.

For each data point, we additionally noted any observed behavior (e.g. social interactions, courtship, tadpole transport, egg deposition, feeding). Courtship behaviour was assigned when the female was following a male producing a courtship call (Stückler et al., 2019). After each courtship, we assigned a number to the clutch, recorded the exact location of the oviposition site and captured and identified the mating partner.

2.4. Data analysis

2.4.1. Software & Statistics

All spatial field data were recorded directly on a tablet PC (WinTab 9, Odys, Willich, Germany) using using a high-resolution map of the island in the mobile GIS software ArcPad 10.2 (ESRI, Redlands, CA, U.S.A.). Data processing was done in ArcMap 10.4 (Coordinate Reference System (CRS): WGS 84/UTM zone 22N; Authority ID: EPSG:32622) (visualization, distance measurements, creation Minimum Convex Polygons), QGIS 3.2 (CRS = EPSG:32622) (creation of Voronoi polygons, extraction of X and Y coordinates for each data point) and the 'adehabitatHR' and 'adehabitatLT' package of 'R studio' (distance between consecutive relocations, trajectory analysis, home range analysis) (Calenge, 2006; R Development Core Team, 2008). All statistical comparisons and illustrations were done in 'R Studio'. The distribution of all sets of data was checked visually (histogram) and statistically (Shapiro.test). All illustrations were edited and compiled in Inkscape 0.92.3.

2.4.2. Female activity patterns

We determined the 'reproductive status' of each female for each tracking day: days without any reproductive behavior were termed 'no courtship' (NC). Courtship in *A. femoralis* typically spans 2 days: it starts on the first day (termed C1) with a prolongated 'courtship walk' where the female follows a male emits courtship calls (Stückler et al. 2019; this study). The couple typically spends the nights under the same leaf. On the morning of the second day (termed C2), they continue the courtship walk for a short while before they choose a site for mating and clutch deposition.

For each female (n=17), we grouped distances between consecutive relocations according to the hour of the day and calculated a mean distance for days without courtship and mating (NC), the day of courtship initiation (C1) and the mating day (C2). Mean values from all females (n = 17) were used to calculate an average distance per hour of the day on NC, C1 and C2 days.

2.4.3. **Female movement in relation to weather conditions**

The X and Y coordinates for each spatial relocation point were extracted in QGIS (v3.2.3). Distances between consecutive relocations were extracted using the 'adehabitatHR' and 'adehabitatLT' package of 'R studio'. All extracted distances moved by an individual frog during the day were used to calculate the 'daily distance'. Temperature and rainfall were measured every 30 minutes by the 'Nouraflux' station located at the Canopy Operating Permanent Access System (COPAS) in direct vicinity to the camp Pararé. Rainfall was averaged over the whole day (including night time) as rainfall during the night contributes to the relative humidity during the daytime and might influence the movement of the frogs. Temperature was averaged over the daylight time (between 6.30 and 18.30), which approximately corresponds to the active period of the frogs.

All females were included into the analysis (n = 17). We tested the correlation between the moved distances per day (m) and average temperature during day (°C) as well as average rainfall per day (mm) using a Spearman correlation (RStudio, cor.test function).

To test whether courtship and mating took place on days with more precipitation, we compared the amount of rainfall for courtship and non-courtship days. All females where we observed courtship were included into the analysis (n = 12). We calculated a linear mixed model (function 'lmer' from R package 'lme4' and 'lmerTest'). For every female, we calculated the mean rainfall per day (excluding nights) on 'courtship' as well on 'no courtship' days. The reproductive status was included into the mixed model as fixed factor, while the identity of the female ('ID') was included as a random factor.

2.4.4. **Female movement in relation to reproductive state**

The 'reproductive status' of each female for each tracking day was determined as explained in 2.4.3. In this analysis we included only females for which courtship was observed (n = 12) and calculated differences between days with (C1 and C2, termed C) and without (NC) reproductive behavior with a linear mixed model (function 'lmer' from R package 'lme4' and 'lmerTest'). For every female, we calculated the mean distance moved on 'courtship' as well on 'no courtship' days. The reproductive status was included into the mixed model as fixed factor, while the identity of the female ('ID') was included as a random factor. In addition, we compared the mean distance moved on C1 to the mean distance moved on C2 with a paired t-test. The variance between the respective grouping variables (C and NC or C1 and C2) was controlled with a levene test ('levene.test', R package 'lawstats').

2.4.5. **Female home range (HR)**

Algorithms estimating home range

According to Burt (1943), the area traversed by the animal during its normal activities of foraging, mating and caring for young constitutes the home range. Multiple analysis algorithms have been proposed to estimate the home range of an individual but numerous analysis algorithms. Among the most common methods for home range assessment are the Minium Convex Polygon method (MCP) and the Kernel Utility Density estimation (Kernel UD) (Calenge, 2006; Cumming & Cornélis, 2012), enclosing all or a 'peeled' percentage (e.g. 95 % isopleth) of animal re-sightings. The most conservative method for home range estimation, the minimum convex polygon (MCP) (Mohr, 1947) is widely used but does not distinguish between high- and low-use areas. The Utilization Distribution function (UD) (Worton, 1989) on the other hand returns the probability density that an animal is found at a point according to its geographical coordinates. Using this model, one can define the home range as the minimum area in which an animal has some specified probability of being located (Calenge, 2006). We estimated the home range with two algorithms to control the robustness of our data: MCP (95 %) as a correlate for already published metrics on poison frog space use and Kernel UD (95 %) for a ecologically more relevant interpretation discriminating between used and non-used areas.

Home range calculations were performed in R (package 'adehabitatHR') using the more conservative minimum convex polygon method including 95 % of data points (MCP95) as well as a classical kernel method including 95 % of data points (Kernel Utility Density (KernelUD95), grid = 200, extend = 1, h = h_{ref}, same for all = FALSE). Differences in the home range size due to application different estimators (MCP95 and the KernelUD95) were assessed with a paired t-test (RStudio, package 'lawstats').

Linear regressions between tracking duration and HR size (MCP95 and KernelUD95) were calculated in RStudio using the lm () function (n = 17). In addition, we repeated the regression analysis with a reduced dataset including only females that were tracked for 14 days or longer (n = 9) were included to

HR in relation to reproductive status

To explore how the home range changes over time, we calculated the cumulative home range with two different methods (MCP95 and KernelUD95) for every day of tracking. For example, tracking days 1-3 were included in the home range estimation for day 3, while days 1-10 were

taken into account for the calculation of the home range for day 10. The minimum number of 9 data points necessary to calculate the KernelUD95 with the R package 'adehabitat HR' was reached after the second day of tracking. Due to the very low amount of data points, home range was typically highly overestimated with KernelUD95 on day 2 compared to calculations including three or more tracking days. We therefore reported the KernelUD home range starting from tracking day 3. To monitor changes in the home range associated with mating events, we determined the 'reproductive status' of each female for each tracking day (as described in 2.4.4) and calculated the mean change in home range for 'courtship' as well on 'no courtship' days. Females were included into the analysis when the complete reproductive sequence (courtship and mating) was observed (n = 11). The reproductive status was included into the linear mixed model as fixed factor, while the identity of the female ('ID') was included as a random factor. The variance between the grouping variables was controlled with a levene test ('levene.test', R package 'lawstats').

Home range without mating

Only females with observed courtship and mating events during the tracking period were included in this analysis (n = 11). We excluded days with courtship and mating (C1 and C2) and calculated MCP95 and KernelUD95 from the original as well as from the reduced dataset using the 'adehabitatHR' package (RStudio). We compared the size to the home range with and without mating events for each female, averaged it and determined the mean percentage of area by which home range declines if courtship and mating are disregarded.

Female centers of use

Based on Wilson et al. (2010), we defined 'centers of use' as an area with a greater density of use than other areas within a frog's home range. We used consecutive isopleths of 5 % difference (5 % - 100 %) of the utilization distribution of the kernel density estimates to visually distinguish areas with dense use for each female. The 30 % isopleth was found to distinguish the highest number of centers per frog while correlating well with visual clusters of relocation points, indicating areas of greater intensity use rather than mathematical artefacts. We defined the KernelUD30 area as female 'center of use'.

2.4.6. **Female trajectories**

The X and Y coordinates for each spatial relocation point were extracted in QGIS. Distances between consecutive relocations were extracted using the and 'adehabitatLT' package of 'RStudio'.

We stated the 'total tracking time' as well as the 'daytime tracking time' excluding the night hours where the frogs typically rest under a leave without moving. All extracted distances moved by an individual frog during the day were used to calculate the 'daily distance'. We used the daily distances to determine the 'mean', 'minimum' and 'maximum' daily distances as well as the 'total' distance' for the complete tracking duration of each individual. The mean total/daily distances of all females (n = 17) were averaged to yield an 'average total/daily distance'. To determine the 'average movement per hour', the 'total distance' was divided by the total hours of tracking for each frog and averaged over all individuals (n = 17). The distance between the two most distant point of the trajectory was extracted in ArcMap 10.4.

For the illustration of the female trajectories, we overlaid their paths with 'Voronoi' estimations of surrounding male territories. This method partitions an area (the island) into regions ('territories') based on equidistant midlines between pairs of points (Voronoi, 1908). The 'Voronoi' polygons were calculated using the function 'Voronoi tessellations' (QGIS) for all males in close vicinity to the respective female during the tracking period. Only the 5 most recent male capture points were included into the creation of the polygons. As the shore of the island is rather steep and not occupied by A. femoralis, we truncated the outer territories midway between a male's outermost locations and the island shore, by adding the vertices of the island outline to the points used in the Voronoi tessellation.

Time budget

We further analysed the female trajectories in relation to the 'centers of use' and determined the percent of time spent by each frog on the following movement categories: relocations in the 'centers of use' (C1-C3), 'sallies' outside the centers of use not directly followed by a courtship event, male directed movement followed by a courtship event ('pre-mating movement') and movement from the egg deposition site until reaching a center of use ('post-mating movement'). The initial movement after tagging, before reaching a center of use, was treated as own category as we couldn't assign this movement to 'sallies' or 'post-mating movement' or to another 'center of use' that was not identified during the tracking. Initial movement was not assigned if the first capture point of the female was already located inside a center of use. Each point of the trajectory was assigned to one of the categories listed above. Points of the same category were summed up and the percent of time spent on the category was calculated by relating the number of points per behavior to the total number of relocation points collected for the respective frog.

Influence of number of surrounding males on female spatial characteristics

We counted the mean density of male individuals located in a 35 m radius of each female center of use.

To create a male density kernel, we used all male CR points that were not associated with tadpole transport and the "Kernel Density" function ($h = h_{ref}$) in the (Spatial Analyst Tools, ArcGIS) with a raster cell size of 0.2 x 0.2 m and a search radius of 35 m as described in (Ringler, Hödl, & Ringler, 2015)). The density values for each male were extracted with the "Zonal Statistics as Table" tool (Spatial Analyst, ArcGIS) and joined with the female KernelUD30 shapefile.

We calculated linear regressions to correlate the mean male density with (1) the size of the centers of use, (2) the number of resting sites and (3) the percent of time spent on sallies of the respective female.

Approach of previous egg deposition site

We checked whether females approach their previous clutches by calculating the distance to the first observed egg deposition for all females with the 'Distance Matrix'-tool (QGIS). A nearing of < 2.5 m to the first clutch was defined as 'approach'. We analyzed if females approached clutches, on which occasion and after which time. Additionally, we calculated the distance between consecutive clutches from one female using the 'Measure Line' tool (QGIS).

Stability of tracking HR over longer periods- comparison of tracking and CR dataset

We compared home range calculations from the tracking (up to 17 consecutive days) and the CR dataset (up to 71 days) to control for the stability of the HR over periods exceeding the track time. We used the minimum convex polygon method including 100 % of data points (MCP100) instead of MCP95 because of the lower number of capture points in the CR dataset. CR data were collected between 24. January and 14. April 2016 (see 2.3.1.) while tracking data were gathered for a maximum of 17 consecutive days during this period.

We calculated MCP areas including 100 % of data points (MCP100) of females that were tracked and for which at least 4 CR datapoints were collected in the CR datasets (RStudio, package 'adehabitatHR'). We determined the percentage of overlap between the shapefiles created from the tracking and the CR dataset using the 'intersect' tool (QGIS). As the polygons created from the CR dataset were mostly smaller than the polygons created from the tracking data, we reported the intersected area as percent area from the tracking area.

Additionally, we compared the averaged home range size (MCP100) from all females represented by 4 or more capture points (n = 23) to the averaged home range size of all tracked females (n = 17).

2.4.7. General findings

We reported general findings and examined whether tagged females show the same behavioral repertoire than females without a tag. We oriented on natural behavior as described in previous publications (Table 1) and compared the findings to the presence/absence of the behaviors of female *A. femoralis* equipped with a tag. As reproductive traits differ considerably between different *A. femoralis* populations (e.g. different rate of male rejection during courtship, Stückler et al. 2019), we focused on behaviors described for the same (e.g. Stückler et al., 2019) or nearby populations.

Table 1: Characteristics and key behaviors of female A. femoralis in natural populations. The following characteristics and behaviors were described for wild *A. femoralis* females and serve as qualitative reference for tagged females.

Category	***Characteristics & behaviors***	***Reference literature***	***Description***
General	Feeding	(Parmelee, 1999)	Food quality: orthopterans, coleopterans, adult arthropods, ants /mites, larvae
	Site fidelity	(Ringler et al., 2009)	Intra-annual female site fidelity
Reproduction	Temporal patterns of courtship	(Stückler et al., 2019)	Courtship starts in the afternoon ~17h and continues on the next morning, ending in mating
	Amplexus	(Stückler et al., 2019)	Cephalic amplexus
	Oviposition	(Stückler et al., 2019)	Oviposition in the morning, ~8h
	Discontinued courtship	(Stückler et al., 2019)	2 out of 29 females discontinued the courtship
Social	Agonistic interactions with females or males	(Ringler et al., 2009; Roithmair, 1992, 1994)	No agonistic interactions observed
Parental care	Tadpole transport	(Ringler, et al., 2015; Silverstone, 1976)	Female compensate for absent male and shuttle tadpoles (7.8 % in the field)
Decease	Predation	(Beck et al., 2017; Pašukonis et al., 2014; Ringler, Ursprung, & Hödl, 2010)	Snakes and spiders described as predators
	Survival rate	(Ringler et al., 2009)	Inter-annual survival < 20 %

3. RESULTS

The total study population of 2016 encompasses 85 males and 82 females. We tracked a total of 17 females equipped with a reflector tag for periods ranging from 6 to 17 days. Eleven females were first captured in 2016, 5 were known from 2015 and one female was captured for the first time in 2014.

3.1. Female activity patterns

Females moved on average shorter distances on days without courtship or mating (n = 176, mean = 0.75 ± 0.22, max = 1.26 m/h, min = 0.48 m/h) with maximal movement observed between 17 h and 18 h. They moved longer distances on days of courtship (C1) and mating (C2). On days of courtship initiation, moved distances peaked in the late afternoon between 16 h and 17 h (n = 122, mean = 1.41 ± 0.91, max = 3 m/h, min = 0.28 m/h), while maximal distances were covered between 10 h and 11 h on mating days (n = 117, mean = 1.86 ± 0.96, max = 3.49 m/h, min = 0.54 m/h). Courtship events always started in the afternoon, mostly between 16 h and 17 h (n_{gesamt} = 15; $n_{15h\text{-}16h}$ = 4, $n_{16h\text{-}17h}$ = 6, $n_{17h\text{-}18h}$ = 5), while eggs were deposited in the morning, mostly between 9 h and 10 h (n_{gesamt} = 15; $n_{before\ 9h}$ = 4, $n_{9h–10h}$ = 8, $n_{after\ 10h}$ = 3). Egg deposition on the mating day is reflected by sudden decrease in movement (Fig. 2).

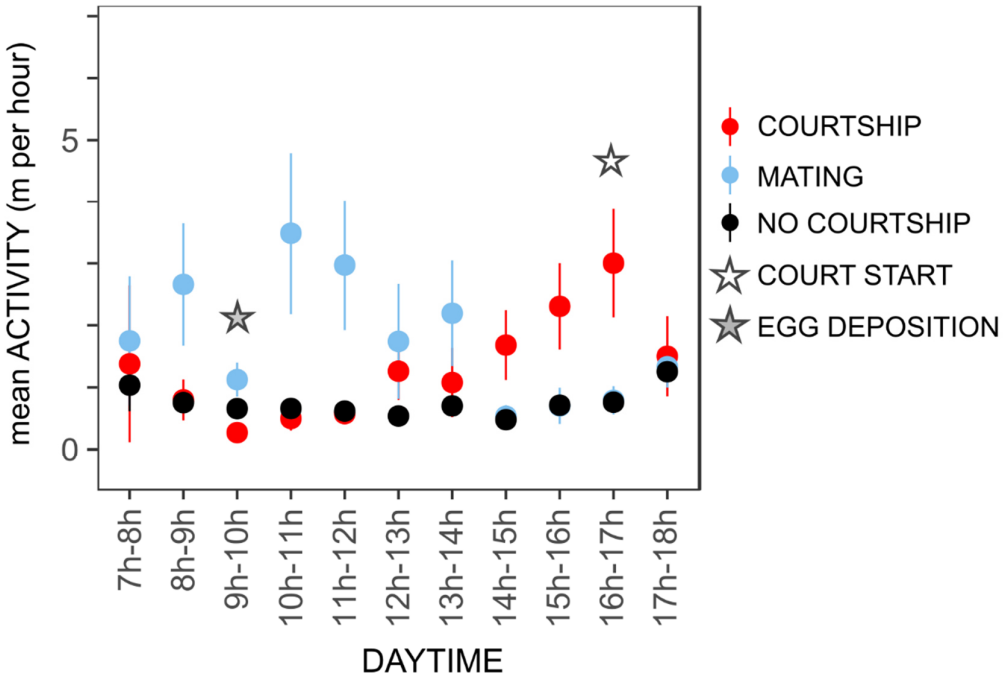

Figure 2: Female activity patterns throughout the day. We calculated the mean distance traveled per hour of the day for each female and averaged it over all study subjects ('mean activity', n = 17). The mean activity throughout the day is shown for days without courtship (black), on the day of courtship initiation (red) and on the mating day. The most frequent hour of courtship initiation is marked with a hollow star, the most frequent hour of egg deposition is indicated by a grey star.

3.2. Female movement in relation to weather conditions

Daily distances moved by female *A. femoralis* showed a significant correlation with both, temperature during day (°C) and rainfall per day (mm). While females moved less on days with higher mean temperatures (Spearman's rank correlation; rho = -0.35, slope = -0.58, p = 0.001), daily movement increased slightly on days with higher mean precipitation (Spearman's rank correlation; rho = 0.36, slope = 0.02, p = 0.002) (Fig. 3). Rainfall on courtship and mating days didn't differ significantly from precipitation on days without courtship/mating (Linear mixed model, n = 12, estimate = - 2.8, SE = 1.7, df = 22, t =- 1.6, p = 0.119).

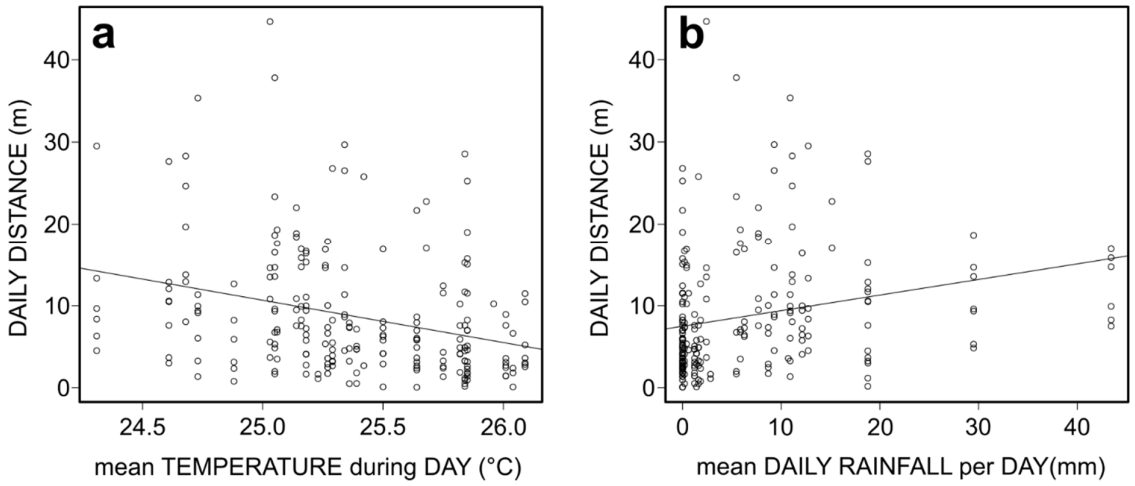

Figure 3: Environmental factors influencing movement. The correlation between the moved daily distances and the environmental factors **(a)** 'temperature' and **(b)** 'rainfall' is shown. We found a significant correlation with both variables. While temperature was negatively correlated with movement of *A. femoralis* females (Spearman's rho = -0.35, p = 0.001), rainfall showed a positive correlation (Spearman's rho = 0.36, p = 0.002), as represented by the linear regression lines.

3.3. Female movement in relation to reproductive state

Females of *A. femoralis* moved significantly longer distances on days with than on days without courtship or mating (Linear mixed model, n = 12, estimate = -8.53, SE = 1.59, df = 11, t = -5.37, p = 0.0002) (Fig. 4**Figure** , a). The average distance moved per day was 7.8 m on days without courtship (n = 12, mean = 7.8, min = 3.9, max = 11.4) and 16.3 m on days with courtship (n = 12, mean = 16.3, min = 8.7, max = 24.3). Distances traveled on the day of courtship and on the day of mating didn't differ significantly (paired t-test, n = 11, t = - 0.85, df = 10, p = 0.41).

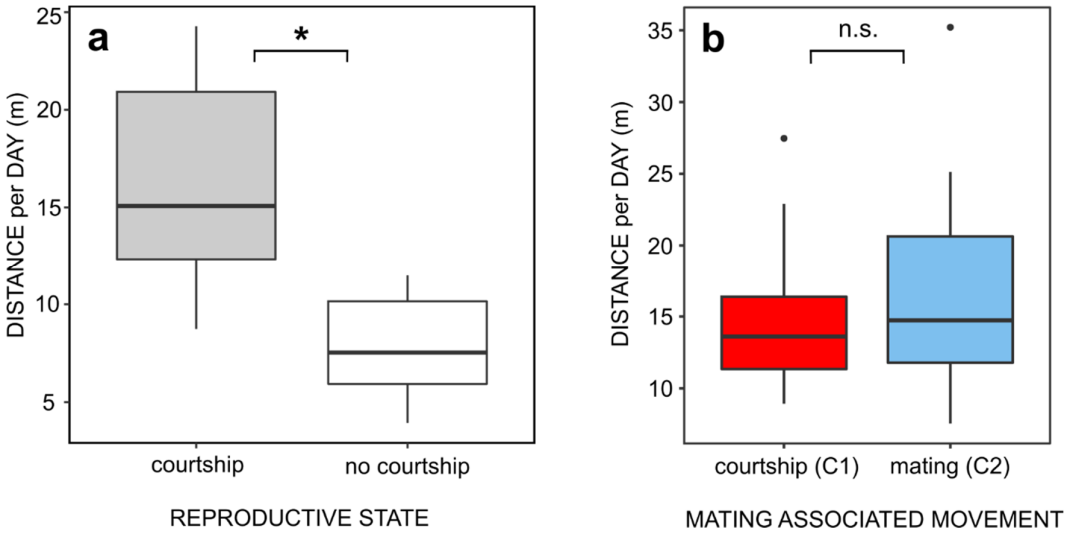

Figure 4: Movement in relation to reproductive behavior. **(a)** Females moved significantly more on days associated with reproductive events compared to days without courtship or mating (Linear mixed model, p =

0.0002). **(b)** Mating associated movement didn't differ between the day of courtship start (C1, red) and the mating day (C2) (paired t-test, p = 0.41).

3.4. Female Home Range

The estimated home range (HR) of female *A. femoralis* ranged from 6.3 m^2 (f09, tracking duration = 38 h) to 419.1 m^2 (f16, tracking duration = 148.1 h) as estimated with MCP95 (n = 17, mean = 107.4, SE = 108.7) and from 30.3 m^2 (f08, tracking duration = 60 h) to 657.6 m^2 (f16, tracking duration = 148.1 h) as estimated with Kernel UD (n = 17, mean = 215.3, SE = 180.9) (Fig. 5).

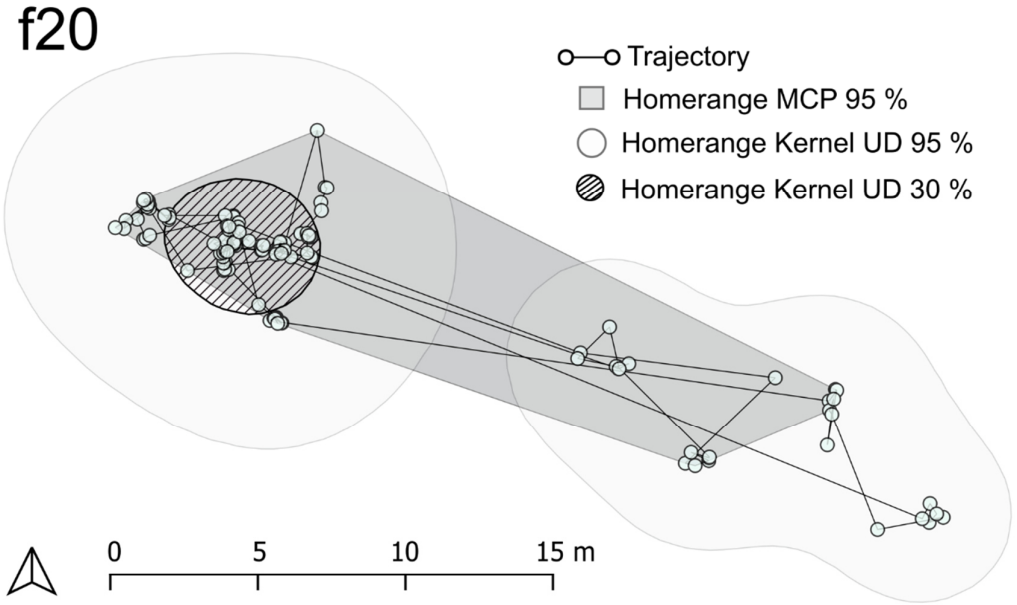

Figure 5: Home range estimation. Datapoints of a representative female (f20, 17 tracking days) are mapped to visualize the two applied models of home range estimation: the more conservative Minimum Convex Polygon calculation (MCP95) is shown dark grey while the home range estimation calculated with KernelUD95 is depicted in light grey. The KernelUD30 area was defined as center of use (striped).

Both home range estimates showed a significant correlation between the covered area and the total tracking time (n = 17, linear regression, MCP95: slope = 19.93, R^2 = 0.2719, p = 0.006, KernelUD95: slope = 22.7, R^2 = 0.2719, p = 0.019). However, no significant differences between area and tracking time were found if only females tracked for 14 days or longer were included into the analysis (n = 9, linear regression, MCP95: slope = 2.39, R^2 = - 0.09, p = 0.58, KernelUD95: slope = 4.23, R^2 = - 0.075, p = 0.53).

The area covered by different females after an equivalent number of tracking days (14 days, n = 9) ranged from 24.8 m^2 (f18) to 285.2 m^2 (f16) as estimated with MCP95 (n = 9, mean =

123.07, SE = 88.85) and from 59.7 m^2 (f21) to 564.9 m^2 (f16) as estimated with Kernel UD (n = 9, mean = 236.2, SE = 172.5) (Table 2).

Table 2: Home range comparison after 14 days. Estimated home range for 9 female *A. femoralis* after 14 days of continuous tracking are reported, the number of reproductive events at this time is indicated as 'Courtship'. Minima are indicated in orange, maxima are marked in blue.

Individual	Courtship	Home range MCP95 (m^2)	Home range KernelUD95 (m^2)
f18	**1**	**24.8**	64.7
f21	**2**	26.8	**59.7**
f15	1	51.2	91.5
f5	2	101.3	175.4
f14	2	104.4	242.3
f20	1	114.3	250.1
f3	2	192.9	447.5
f6	1	206.7	229.7
f16	**1**	**285.2**	**564.9**
Mean	-	123.1	236.2
Median	-	104.4	229.7
SE	-	88.8	172.5

Consistently, a larger home range was assigned by the KernelUD95 estimation (Table 2). At the 95 % isopleth, the Home range area described with MCP was on average 56.7 % smaller than the kernel density estimate.

The size of female centers of use (KernelUD30) was weakly correlation with total tracking time (n = 17, linear regression, slope = 18.6, R^2 = 0.179, p = 0.05). The correlation was lost if only females tracked for 14 days or longer were included into the analysis (n = 9, linear regression, slope = 1.8, R^2 = - 0.122, p = 0.72).

Home range in relation to reproductive behavior

Independent of the method applied for home range estimation, the change in female home range was significantly higher on days were courtship or mating was observed as compared to days without courtship or mating (linear mixed model, n = 11; MCP95: estimate = -10.4, SE = 4.421, t = -2.363, p = 0.0397; KernelUD: estimate = -24.7, SE = 11.53, t = -2.14, p = 0.044). Accordingly, alterations in the estimated home range of the respective females were mostly (Fig. 6 a, c, d, e, f) - but not exclusively (Fig. 6 b, e) – associated with reproductive events (courtship or mating). Most females showed the highest change in home range directly on the days of the reproductive event (Fig. 6 a, c, d). One female was observed initiating a second mating event immediately after failed egg deposition with her first partner (f14, 6 d).

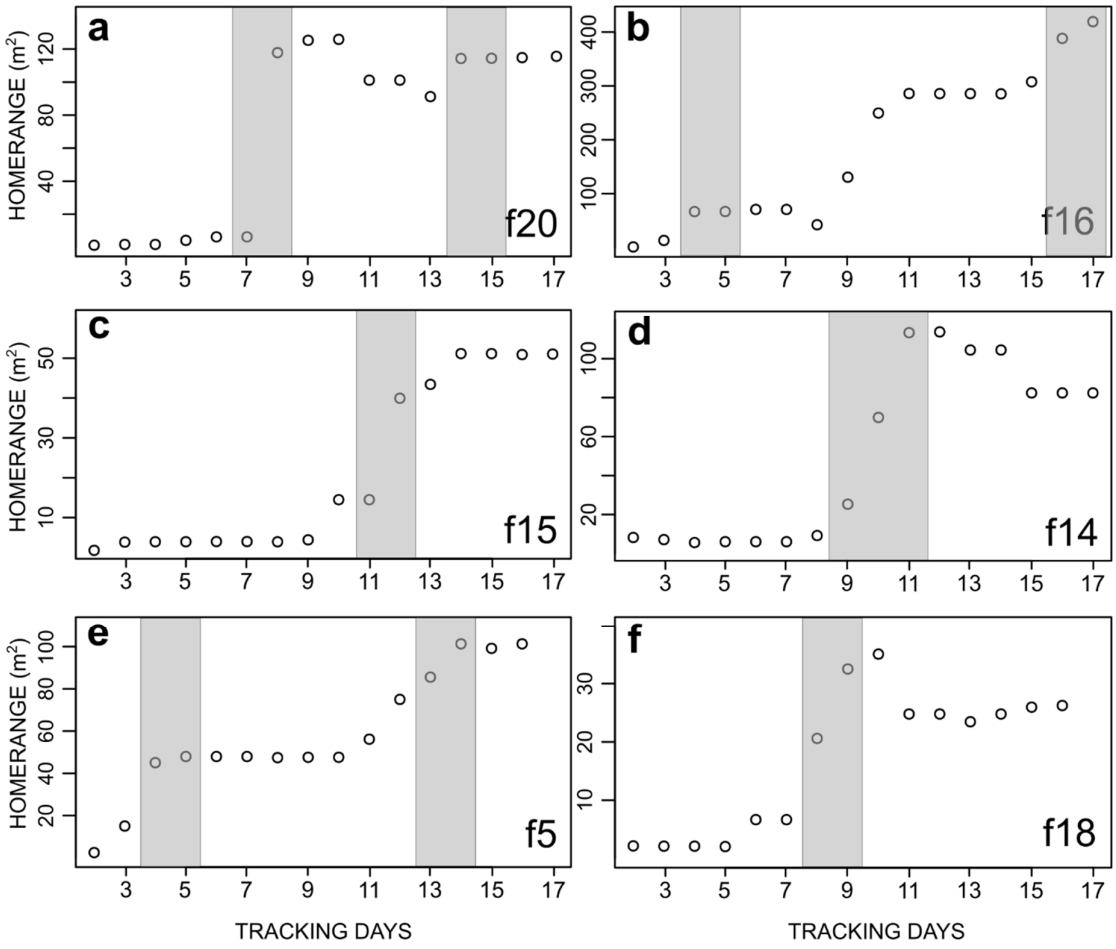

Figure 6: Home range in relation to reproductive behavior. The development of the home range (MCP95) per tracking day is shown for 6 females tracked for at least 16 days. Grey bars indicate reproductive events (courtship-mating) which typically span two days. Home range estimations using KernelUD95 showed similar patterns. Most females showed the highest increase in home range size on the days of courtship and mating (a-f).

Home range without mating

HR excluding courtship and mating ranged between 18.3 m^2 and 277.9 m^2 when estimated with MCP95 (mean = 92.5 m^2, SD = ± 97) or 32 m^2 and 412.5 m^2 when estimated with KernelUD95 (mean = 179.5 m^2, SD = ± 134.9).

For both estimators (MCP95 and KernelUD95), HR was on average ~30% smaller when neglecting days with courtship and mating (mean = 69.4 %, SD = ± 32, min = 15.8 %, max = 137.5 % compared to MCP95 area including courtship and mating; mean = 72 %, SD = ± 26.7, min = 11.4 %, max = 108.6 % compared to KernelUD95 area including courtship and mating).

3.5. Female Trajectories

We tracked females for an average of 108.7 hours during their daylight active period between 7:30 and 18:30 (n = 17; mean = 108.7 h (11 d 6 h); SD = ± 39.2; min = 38.0 h; max = 157.7 h;

average tracking duration including nighttime was 11.6 days (mean= 279.4 h = 11.6 days; SD = ± 102.3). Nights were spent immobile under a leaf and were excluded from further calculations. During tracking, females moved an average total distance of 111.3 m (n = 17; mean = 111.3 m; SD = ± 64.3; min = 18.3 m ; max = 227.0 m; indicated distances not corrected for tracking duration) with an average daily distance of 8 m (n = 17; mean = 8 m; SD = ± 3.5; min = 2.6; max = 14.4). The average cumulative movement per day ranged between 1.6 m (n = 17, mean of minima = 1.6 m; SD = ± 1.3; min = 0.1 m; max = 3,7 m) and 22.2 m (n = 17; mean of maxima = 22.2 m; SD = ± 11.3; min = 6.1 m; max = 44.6 m). Females moved on average 1 m per hour (n = 17; mean = 1.0 m; SD = ± 0.4; min_{mean} = 0.3 m (no mating observed during tracking); max_{mean} = 1.76 m (two mating events observed during tracking). The fastest recorded movement of 24,03 m per hour was related to a subsequent mating event. The average distance between the two most distant points of the individual trajectories was 19.7 m (n = 17; mean = 19.7 m; SD = ± 9.5 m; min = 6.1 m; max = 40.0 m).

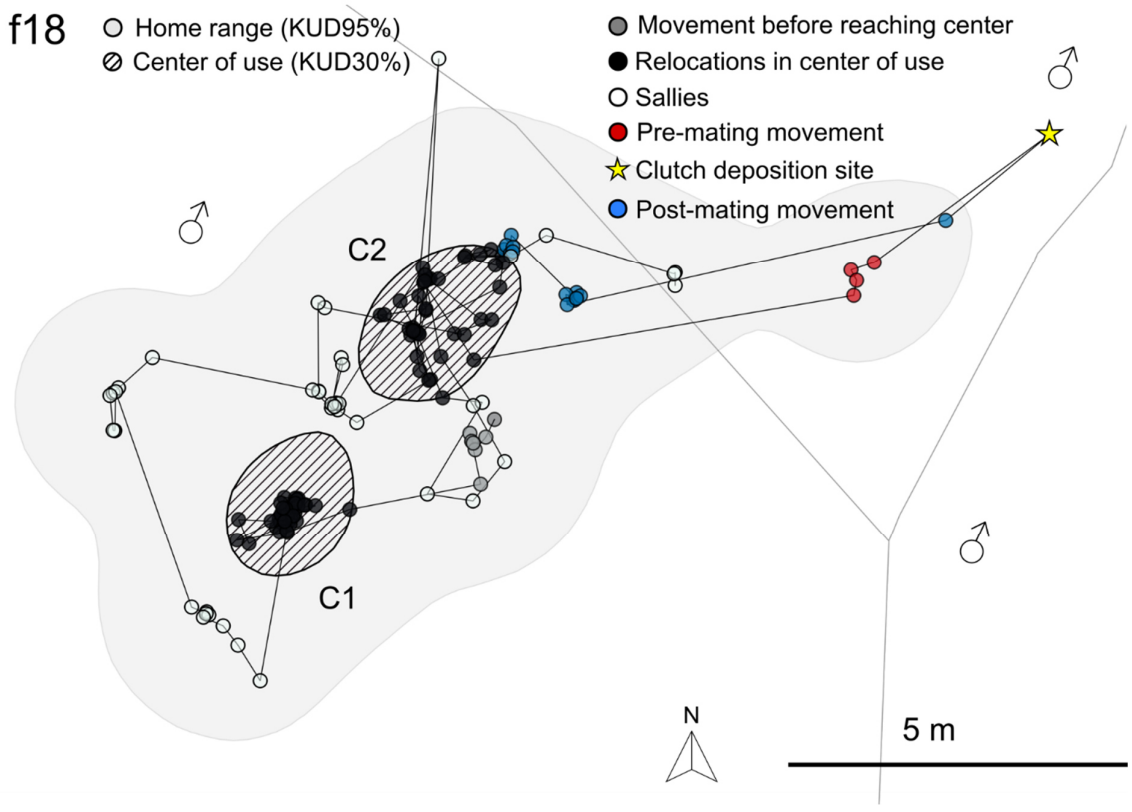

Figure 7: Female trajectory. Representative example (f18) of female trajectory with 2 centers of use. Centers of use (C1, C2) are striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Relocalization points after tagging before reaching a center of use are shown in dark grey. Datapoints in the center of use are indicated in black, sallies to the surrounding are hollow, pre-mating movement is indicated in red and post mating movement until the next center of use is reached with blue dots. The egg deposition site is indicated by a yellow star. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol.

Females had up to three centers of use but most of them returned to one center during the tracking (n_{gesamt} = 17, n_{c1} = 12, n_{c2} = 3, n_{C3} = 2). Centers were on average 9.4 m apart (n = 9, mean = 9 m, SD = ± 3.6 min = 3.4 m, max = 14.2 m) with an average size of 20.7 m^2 (n = 17, mean = 20.7 m^2, SD = ± 18.8, min = 2.4 m^2, max = 66 m^2). The number of sallies varied between 0 and 12 (n = 17, mean = 4.3). All females deposited their eggs outside of their center of use. 3 out of 4 females who mated with the same male used one center while 3 out of 4 females who had different mating partners had more than one center of use. One was excluded from the interpretation because she switched mating partners after unsuccessful mating on the same day. The remaining two females didn't choose a center of use closer to the territory of the following mating partner but used a center further away before moving back and starting courtship.

Female time budget

Females spent on average 61.9 % (n = 17, SD = ±10.1, min = 46 %, max = 79.8 %) of their time in the centers of use, 19.8 % (n = 17, SD = ±10.8, min = 0 %, max = 37 %) on sallies to the surrounding area and 9.1 % (n = 17, SD = ± 7.9, min = 0 % , max = 24.6).

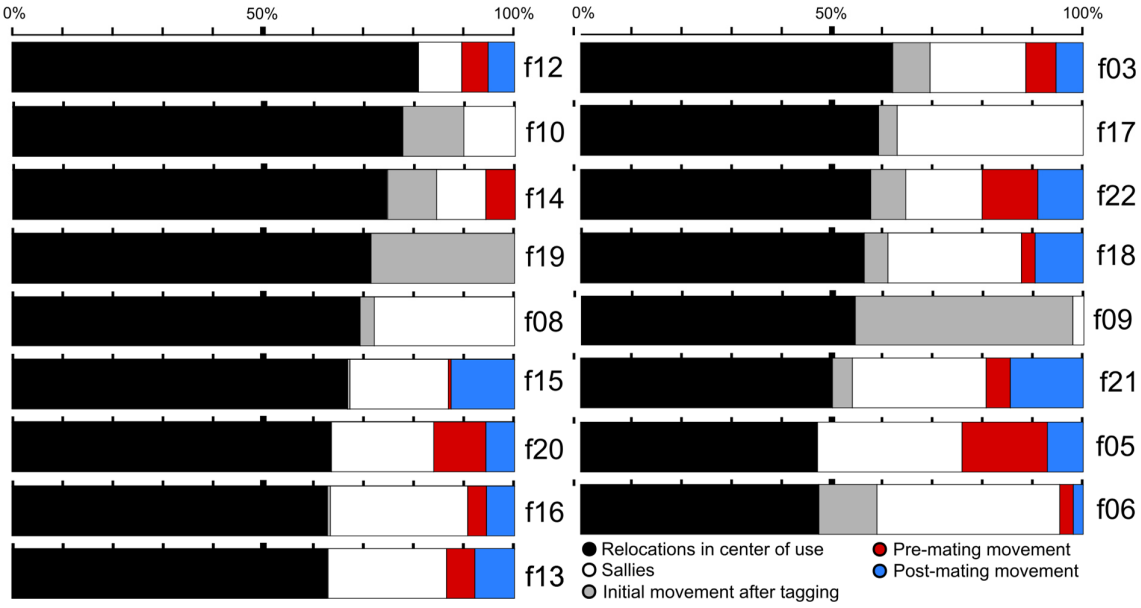

Figure 8: **Female time budget.** The percentage of time spent (i) on movement after tagging before reaching a center of use (grey), (ii) in the center of use (black), (iii) on sallies outside of the center (white), (iv) on pre-mating movement towards a mating partner (red) and (v) on post-mating movement until reaching the next center of use (blue) is illustrated.

Influence of density of surrounding males on female spatial characteristics

Neither the size of female centers of use, nor the number of resting sites was correlated to the mean density of males in their surrounding (KernelUD30 size: linear regression: n = 17, SE =

13.9, slope = - 2.3, R^2 = - 0.035, p = 0.51; Number of centers: Spearman correlation: n = 17, S = 753.7, rho = 0.08, p = 0.8). Similarly, we found no correlation between the mean male density and the percent of time that females spent in the center of use or on sallies (linear regression: time spent in centers of use: n = 17, SE = 13.6, slope = 0.37, R^2 = 0.01, p = 0.28; percent of time spent on sallies: n = 17, SE = 14.1, slope = 0.06, R^2 = - 0.06, p = 0.86).

Approach of previous egg deposition site

Although no female was observed to attend a clutch, 6 out of 11 females were found in proximity (< 2.5 m) to their first clutch again during tracking. Females revisited the area after different time periods (min = 4 d 23 h, max = 11 d 8 h) but mostly (5 out of 6) during another courtship/mating. 3 out of 6 females passed by the previous clutch during the next courtship before mating with the same male again. Another female visited the first deposition site on a sally that was directly followed by a courtship. One female who chose a different male for the second mating detoured past the previous oviposition site on her way back to the center of use after mating, a second female revisited the first egg deposition site during a sally.

Clutches from the same partner were on average 1.8 m apart (n = 3, mean = 1.8 m, min = 0.8 m, max = 3.1 m), while clutches with different males were on average 8.7 m apart (n = 2, mean = 8.7 m, min = 7.6 m, max = 9.8 m).

Are tracking data representative for female long-term home range?

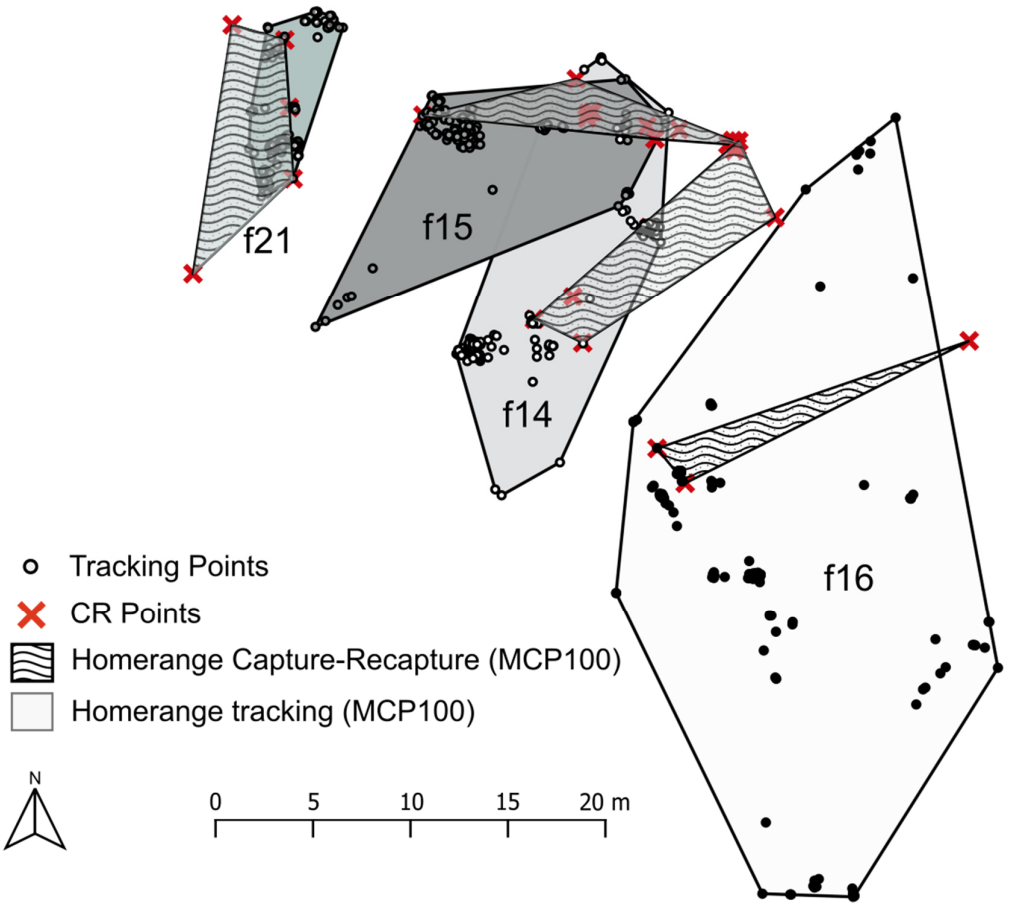

Figure 9: Long term site fidelity represented with short term tracking. MCP areas calculated from tracking and CR dataset are shown for 4 females. MCP100 Polygons for the respective female from the 2 datasets always overlapped. CR capture points are marked with a red cross, tracking points are shown as dots. Tracking MCP100 polygons are shown in plane colors (white, light grey, dark grey, green-grey) while corresponding CR MCP100 are shown in the same color but with wavy fill.

MCP100 polygons created with CR dataset (time span: 24. January and 14. April 2016 only females with ≥ 4 capture points) and tracking dataset (up to 17 days) always overlapped (n = 9, mean = 46.8%, SD = ± 41.27, min = 8.7 %, max = 136.5 %). For all but one female the MCP100 area was smaller when calculated from the CR dataset as compared to the tracking (Table 3). The same pattern was found when comparing MCP100 areas of all females of the island with over 4 capture points to MCP100 areas calculated from tracking (CR: n = 23, mean = 74.7 m^2, SD = ± 108.9, min = 1.7 m^2, max = 436.7 m^2; tracking: n = 17, mean = 138.7 m^2, SD = ± 129, min = 9.9 m^2, Max = 485.7 m^2). The mean tracking MCP100 HR was on average 1.9 times larger than HR areas calculated from the mean CR MCP100 HR.

Table 3: Home range estimations from different datasets. Only females with more than 4 capture point in the CR dataset were included into the analysis. Home range for CR and tracking dataset was calculated with MCP method using all datapoints (MCP100). Shapefiles were intersected and the overlap of the polygons was calculated (shown as % of the mostly larger MCP100 area). Tracking duration, number of tracking points and time span of CR data collection (first to last capture point) are shown for each female.

RECCO_ID	CR points	MCP100 m^2 CR	MCP100 m^2 tracking	Tracking duration	overlap %
f13	6; 68 days	18.3	210.6	8 days	8.7
f12	6; 57 days	12.0	86.2	10 days	13.9
f5	11; 65 days	25.2	133.4	16 days	18.9
f15	10; 70 days	21.8	111.6	17 days	19.5
f14	8; 71 days	42.2	137.2	17 days	30.8
f6	5; 67 days	160.9	316.7	16 days	50.8
f19	4; 37 days	17.1	25.9	10 days	66.2
f8	4; 66 days	7.6	9.9	7 days	76.2
f21	5; 42 days	6.0	26.9	14 days	136.5

3.6. General findings and behavioral repertoire of tagged female *A. femoralis*

We confirmed the performance of all key behaviors described for untagged female *A. femoralis* for frogs equipped with a tag.

We observed feeding on six occasions: two females were observed catching a passing ant, on two occasions we witnessed pilfering of prey from termite-raiding ants (genus *Neoponera*) and two females were found fly-catching on fresh howler monkey excreta in their close vicinity.

In line with several studies (e.g. Ringler et al. 2009; Roithmair 1992, 1994) no female engaged in any agonistic interaction, neither intra- nor intersexual. No female was observed attending a clutch, but on one occasion a female was transporting two tadpoles as reported in previous studies (Ringler et al., 2015; Silverstone, 1976). We did not directly witness any predation event (known for snakes (Costa-Campos et al. 2017; Ringler et al., 2010), spiders (Beck et al., 2017) and scorpions (personal observation 2018). The mean number of recaptures per individual during the tracking was 4 (N = 17). Out of 17 females, we found one dead after 6 days without any obvious reason, one was found dead and covered in bees and one tagged female disappeared without trace, suggesting a predation event.

We observed a total of 21 courtship events involving 12 tagged females. For seven females, we observed two courtships during tracking. The average time between two successive clutch depositions by the same female was eight days (n = 7; mean = 8 days; SD = ±2,4 days; min = 5 days; max = 12 days) and the average clutch size was 17.4 eggs (n = 11; mean = 17,4; SD =

±3,8; min = 11; max = 25) confirming Weygolds' observations for captive *A. femoralis* (Weygoldt, 1980). All 21 courtship events ended with a mating attempt on the second day, 19 courtship events ended with a successful clutch deposition: one female was observed in two immediately consecutive courtship events with two different males without successful clutch deposition. Although unsuccessful courtship events were also described by Stückler (Stückler et al., 2019), we removed the tag of the respective female after the second unsuccessful courtship to avoid egg binding potentially prompted by the waistband. Out of seven females who were observed in two successful courtship events during tracking, three mated with the same male twice, three chose a different male for the second mating event and at one occasion, the second male could not be captured and identified after clutch deposition. One more female was caught in courtship with the same male shortly after removing the tag. Two courtship attempts were interfered by other individuals, which was also previously described in other studies (Montanarin et al., 2011; Stückler et al., 2019). On one occasion the approached male started to court a different female, another courtship was interfered by a small male that was approached the courting couple and was subsequently attacked by the male.

Figure 10: Reproduction-related behavior of tagged females. Female *A. femoralis* equipped with a tag (right side) attending a calling male (left side) after actively approaching him. Picture provided by A. Pašukonis.

4. DISCUSSION

Space use differed considerably between individuals, ranging from 24.8 m^2 to 285.2 m^2 after 14 days (MCP95) (Table 2). Although HR increased significantly with the number of observations (Figure a-e) (Odum & Kuenzler 1955), we did not find a significant correlation between HR and tracking time for frogs observed over periods including at least one courtship (longer than 14 days). Courtship and mating accounted for about 30% of the total home range size, indicating that females spent large parts of their time in smaller areas. Ringler et al (2009) described a retreat of female *A. femoralis* to resting sites varying from 0.006 to 10.08 m^2 (Minimum Modified Area, (Ringler et al., 2009). Accordingly, visual inspection of the trajectories revealed clusters of consecutive relocation points that we defined as 'centers of use' that are best represented by the Kernel UD 30% isopleth (Fig. 5 and 7). Females used up to 3 centers during the tracking and spent on average 62 % of their time in areas ranging between 2.4 and 66 m^2. Neither size and number of used centers nor the number of sallies were correlated with the mean density of surrounding males. Thus, females might adapt their fine-scale space use to the immediate behavior rather than the number of surrounding males, e.g. to avoid food competition (e.g. Ward, Webster, & Hart 2006).

The reported home range measures rest far below the areas used by migratory species (e.g. 1900 m^2 in *Bufo bufo* (Sinsch, 1987)) but are larger than described for other territorial leaf-litter poison frogs (e.g. 44 m^2 in *A. trivittata* (Roithmair, 1994; Wells, 2007)) or different populations of *A. femoralis* so far (e.g. 10 m^2 (Ringler et al., 2009)).

Inter- and intra-specific variations in space use need to be considered in a methodological as well as in a biological context: discrepancies in published space use metrics are partly explained by divergent methods for data collection (e.g. CR or tracking) and -analysis (e.g. different definitions and algorithms for home range estimation). For example, the estimated HR was consistently larger when calculated with the tracking dataset than with the CR dataset. We propose, that the difference in HR calculated from tracking and CR datasets arises from the different impact of female inconspicuousness on the two approaches: many female frogs are particularly challenging to survey via CR as they don't engage in any visual or acoustic displays. This can bias CR datasets in two ways: First, CR studies rely on specific behaviors that make the animals more conspicuous, such as male calling or female mating behavior (McKnight & Ligon 2017). For example, *A. femoralis* females can be found by localizing males that emit distinct courtship calls (Stückler et al., 2019). Reproduction associated capture points

(29% of female datapoints) are overrepresented compared to the female time budget (9% on courtship and mating) (Fig. 8) and can bias female HR towards the location of the mating partner. Secondly, the chances of repeated encounters are higher for females who spend their time in one center of use. While absolute size estimations between MCP95 and Kernel95 differed in our study (Fig. 5, Table 2), ecologically relevant patterns (e.g. the increase in home range size on days with courtship and mating) were consistently found with both methods.

Biologically, intra-specific differences in female space use likely originate from population densities, long-term site choice and the availability of resources around the centers of use. Although the habitat at the study site is relatively homogenous, resources like pools, spawning sites, conspecifics or temporary food sources might influence fine-scale movement (e.g. pool availability: *A. paleovarzensis*: Rocha, Lima, & Kaefer 2018; phytotelmata availability: *O.pumilio*: Donnelly 1989; Pröhl & Berke 2001; *R. ventrimaculata*: Poelman & Dicke, 2008; conspecific attraction: *O.pumilio*: Folt et al. 2018; momentary food resources: *A. femoralis*: Ringler et al. 2015; Ringler, unpublished data). For example, *A. femoralis* females deposit their clutches in the leaf-litter abundant throughout the study site but prefer Carapa-leaves when available (Weinlein, unpublished). Temporal availability and quality of resources (e.g. desiccation of natural pools, flies attracted by howler monkey excrements or fungi) as well as knowledge about their location varies and were not considered in this study.

Inter-specific differences in home range size are likely to arise from different parental care strategies and how duties are split between the sexes. For example, the spatial behavior of the Mimetic poison frog *Ranitomeya imitator* is e.g. dictated by a monogamous pair bonding and biparental care, where males and females mutually defend a territory containing breeding pools and care for their young (Brown, Morales, & Summers, 2008; Symula, Schulte, & Summers, 2001). Consequentially, both sexes show a high degree of site fidelity to a home range of ~ 4.6 m^2, with no differences in space use between male and female individuals (Jason L. Brown et al., 2009). In contrast, closely related Amazonian poison frog *R. ventrimaculata* are promiscuous and display male uniparental care (Poelman & Dicke, 2007). Male frogs defend a territory (up to 9 m^2) that is typically smaller than the area used by females (up to 39,3 m^2) that need to search for mates because males are not advertising their presence through vocalizations (Poelman & Dicke, 2008). Male uniparental care is the most ancestral form of caregiving to offspring (Summers & Tumulty, 2014): while males shuttle their tadpoles from terrestrial clutches to aquatic deposition sites, female obligations are confined to oviposition. This form of caring for young is widespread among multiple genera e.g. *A. femoralis and A.*

trivittata (Roithmair, 1992), *R. variabilis* (Brown et al., 2008), *D. auratus* (Summers, 1990). Derived parental care strategies involve biparental care (e.g. *Oophaga pumilio* (Brust, 1993), *R. imitator* (Brown, Morales & Summers, 2009)), female uniparental care as seen e.g. in *D. histrionicus* (Summers, 1992) and varying degrees of caretaking, like clutch guarding before tadpole transport and egg-feeding after deposition. How mating systems and parental commitment drives sex differences in fine-scale spatial behavior should be investigated in a comparative study spanning multiple genera with distinct caretaking strategies.

Why to stay

Short-term tracking of 7-17 days mapped long-term HR of up to 71 days as determined with CR (Fig. 9). These results demonstrate that brief tracking can inform about long-term spatial behavior in *A. femoralis*. Our tracking and CR data confirm female seasonal site fidelity reported by Ringler et al (2009) for a different study area (Table 3).

Site fidelity provides several advantages to *A. femoralis* females: (1) Frogs can reduce energy expenditure and predation risk by minimizing movement (Pough et al., 2015; Ryan, Tuttle, & Rand, 1982). (2) Females compensate for male absence by transporting tadpoles in the field (this study; Ringler et al., 2013; Silverstone, 1976) as well as in laboratory experiments (Ringler et al., 2015). Although the mechanism of female compensation of paternal care remains elusive, staying close to the clutch allows easy survey. Females show homing behavior after induced larval transport (Pašukonis et al., 2017), implying benefits of the home area e.g. experience with the mating partners or enhanced larval survival rate by taking over tadpole transport in case of a male drop-out.

Why & where to go

Our data illustrate significantly increased travel distances on days with courtship and mating, suggesting that reproductive behavior is an important factor in prompting female movement (Fig. 4 a, b). Movement for other purposes than reproduction, e.g. foraging excursions (*D. auratus* (Pough & Taigen, 1990)) or exploratory behavior (described for *O. pumilio* females (Brust, 1990) and *D. auratus* (Summers, 1989), but not *A. femoralis* males (Beck et al., 2017)) was not observed in *A. femoralis* females.

Various factors like previous experience and spatial proximity of the mating partner influence the decision where to move for courtship (Rosenthal, 2017). Females of our study population were shown to rarely reject partners after courtship initiation (Stückler et al. 2019, this study), and to mate with males available within a 20 m distance (Ursprung et al., 2011). Tracked

females mated with a male within 20 m distance in 72% of mating events, supporting closeness as important factor for mate choice. Proximity has previously been proposed as proxy for non-random mate-choice in *A. femoralis* (Ursprung et al., 2011) and in the poison frog *Oophaga pumilio* (Meuche et al., 2013). However, several aspects also suggest active mate-choice based on cues provided prior to courtship: (1) In line with Stückler et al., 2019, all tracked courtships ended with a mating attempt (21/21), implying mate-choice prior to the initiation of courtship, e.g. based on male calls. (2) Sporadic observations showed that females occasionally ignored a male in direct vicinity immediately before travelling long distances to their mating partner. (3) At least half of the females who were observed in two courtships mated with the same male twice, despite the presence of other neighbors.

We did not find any evidence for regular monitoring of previous oviposition sites although female *A. femoralis* occasionally transport their tadpoles (Ringler et al. 2015; this study) and discriminate between kin and non-kin clutches in laboratory settings (Ringler et al., 2016). Females deposited their clutches exclusively outside of their center of use (19/19) and were found in proximity to their previous clutches during or after the following courtship, even if they chose a different partner for mating (Fig. 7, supplementary material). Females who mated with the same male twice deposited the second clutch close to the first one (~ 1.8 m) and were spatially close to their first clutch during the following mating event. Even though we cannot exclude that females occasionally visit their clutches, the observed approaches of previous deposition sites occurred at timepoints before the larvae were ready to carry (15-20 days after oviposition). We therefore suggest that females monitor the presence of previous mating partners rather than the clutch itself.

When to go

We observed different female activity patterns depending on the reproductive state of the frogs (Fig. 2). While movement on non-courtship days was generally low with peaks in the morning and in the evening, females moved preferentially in the afternoon between 16 h and 17 h to initiate a courtship. This timing coincides with heights in male calling activity (peak: 15 h - 16 h, Kaefer et al. 2012 and personal observation 2018), suggesting that females use acoustic cues to tune their motion (Gerhardt, 1991; Sinsch, 2010). Movement after mating peaks at 10 h- 11 h immediately after oviposition, when females leave the mating site and male calling activity is low, indicating that other factors than male vocalization influence the decision where to go after mating.

In line with Bellis et al. (1962) and Beck et al. (2017), we found a significant correlation of the travelled distance per day with both temperature and cumulative rainfall (Figure a, b). Frogs moved more on days with lower mean temperatures, mirroring the fact that high environmental temperatures affect physiological function and influence the behavioral performance of ectotherms (Beck et al., 2017; Bellis, 1962; Navas, 1996; Navas, Gomes, & Carvalho, 2008). Tropical species tend to have narrower thermal tolerances and as habitat temperatures in the tropics are closer to the upper thermal limits of amphibians, frogs are more vulnerable to climatic fluctuations (Bonetti & Wiens, 2014; Duarte et al., 2011; Sunday et al., 2014). Although cumulative rainfall was significantly correlated with female motion, the respective regression slope of 0.02 indicates a weak effect, as conformingly reported for our study species before (Beck et al., 2017). There was not significantly more rainfall on courtship/mating days than on others, indicating that courtship initiation was not immediately triggered by rainfall. However, rainfall is a strong predictor of male calling activity on a seasonal scale (Kaefer et al., 2012). As in many anuran species, male vocal signals in turn have been found to stimulate estrogen changes in females (for review see Wilczynski & Lynch 2011), rainfall likely influences the timing of female movement indirectly via increased male calling activity .

The conventional CR approach is most commonly used for spatial monitoring of animals (Thompson, White, & Gowan, 1998). CR methods are well suited to asses generation-spanning population data, long-term movement and site fidelity (Manning & Goldberg, 2010; Parrish, Stringer, & Sherley, 2014). Tracking is advantageous as it allows to find animals at any time without relying on the random encounter of study objects (Kays et al., 2015; Richards et al., 1994). Tagging small anuran species is tricky: the moist skin of amphibians hampers direct tag attachment by tissue glue, a method commonly applied to small animals. Studies on behavioral ecology of small amphibians therefore employ miniature tags attached with the help of waistbands in combination with telemetry (Fukuyama, Kusano, & Nakane, 1988; Gourret, Alford, & Schwarzkopf, 2011; Mascanzoni & Wallin, 1986; Pasukonis et al., 2013; Pašukonis et al., 2014) (Fig. 1). Even though this tracking technology has been used successfully in *A. femoralis* (Pašukonis et al., 2014), its' suitability for longer-term tracking including several reproduction events was not assessed. The disadvantages of tracking with tags fixed on waistbands are not negligible: frogs need to be captured and manually checked for wounds, localizing them multiple times per day might disturb their behavior and long-term effects of tagging are not known. Tagged females showed all key behaviors (feeding, site fidelity, courtship, mating, amplexus, oviposition, tadpole transport) described for untagged

individuals (Beck et al., 2017; Kaefer et al., 2012; Montanarin et al., 2011; Parmelee, 1999; Pašukonis et al., 2014; Ringler et al., 2009, 2010; Roithmair, 1992, 1994; Silverstone, 1976; Stückler et al., 2019; Weygoldt, 1980) (**Fehler! Verweisquelle konnte nicht gefunden werden.**) (Fig. 10). One witnessed discontinued courtship as well as a mortality rate of 3 out of 17 tracked females could not clearly be attributed to the tag as both happenings were described in non-tagged frogs with comparable prevalence (Ringler et al., 2009; Stückler et al., 2019). It is possible that tagging increases the mortality rate by making frogs more conspicuous to predators and slower in escaping (Kenward, 2001). While we didn't investigate other possible effects of tagging like feeding success, total movement amount or long-term reproductive success (Blomquist & Hunter 2007; Langkilde & Alford 2002; Rowley & Alford 2007), equipping wild *A. femoralis* females with a tag did not alter the behaviors analyzed in this project substantially.

Our study demonstrates how short-term tracking can be used to refine information gathered by a conventional CR approach, filling the knowledge gap about patterns, causation and function of fine-scale spatio-temporal behavior in poison frogs.

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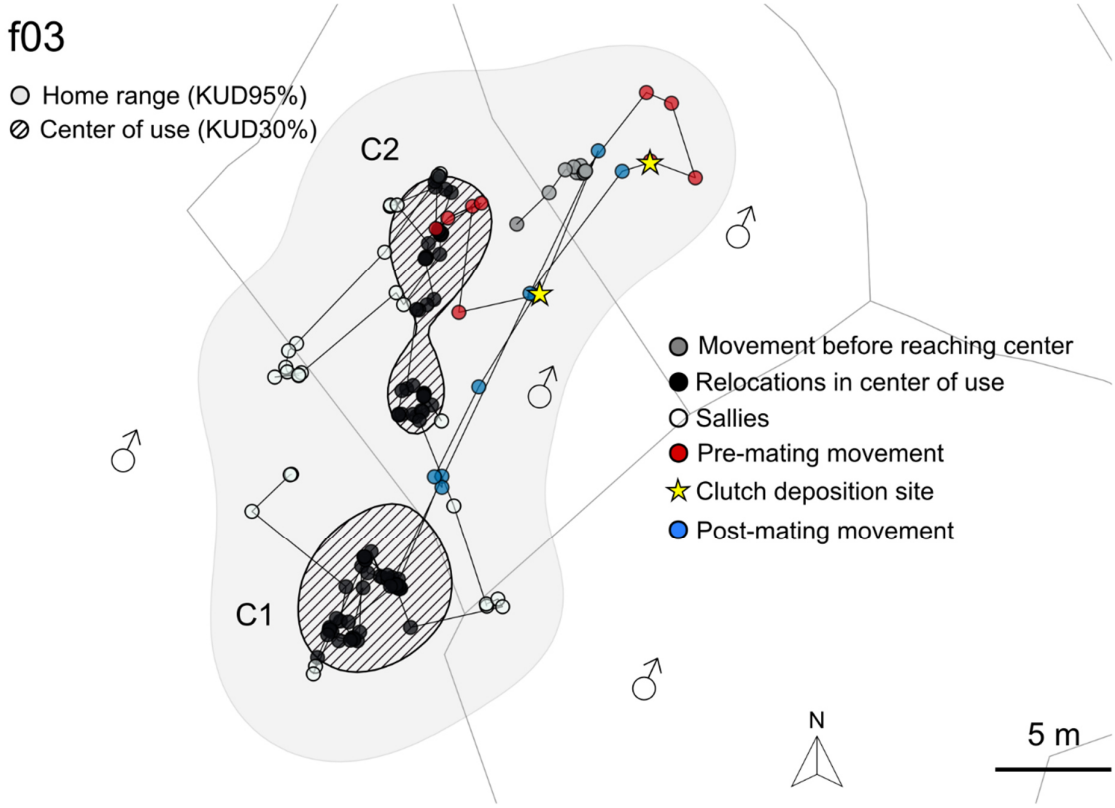
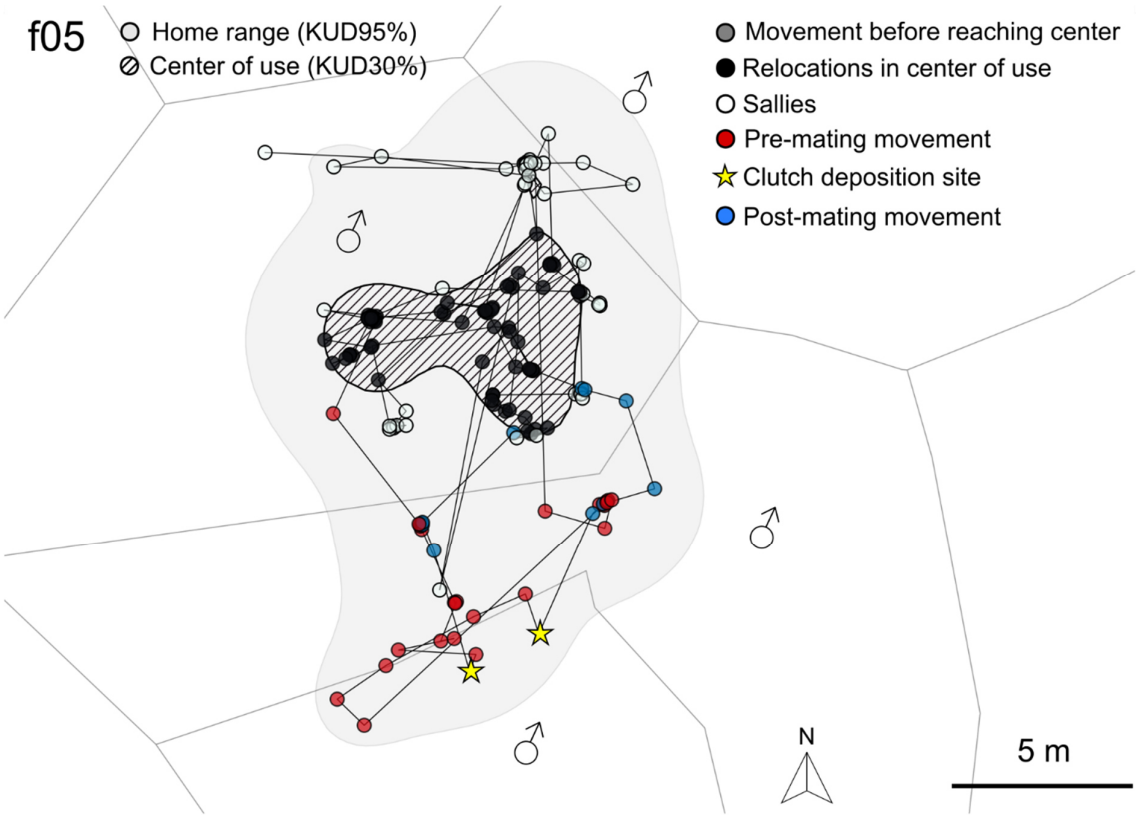
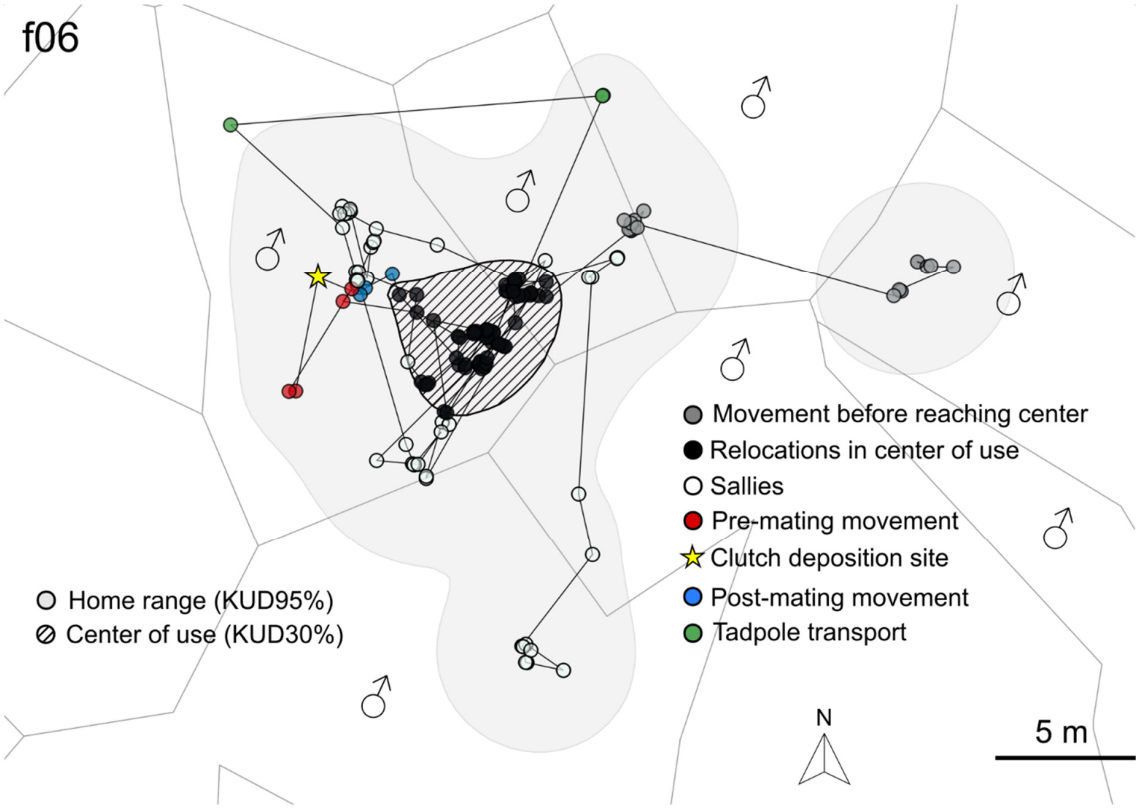
6. SUPPLEMENTARY MATERIAL



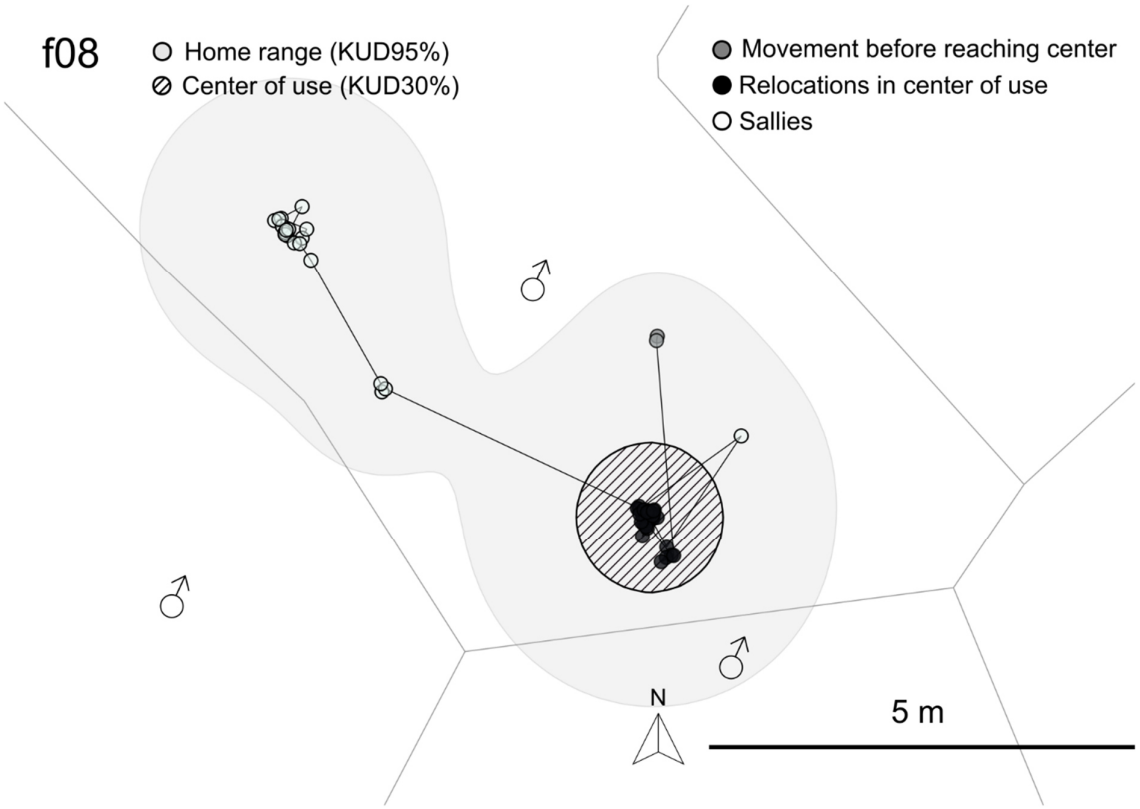
Supplementary Figure 1: Trajectory of female f03. Female trajectory with 2 centers of use. Centers of use (C1, C2) are striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Relocalization points after tagging before reaching a center of use are shown in dark grey. Datapoints in the center of use are indicated in black, sallies to the surrounding are marked with hollow dots, pre-mating movement is indicated with red and post-mating movement until the next center of use is reached with blue dots. The egg deposition site is indicated by a yellow star. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol. This female was tracked for 15 days.



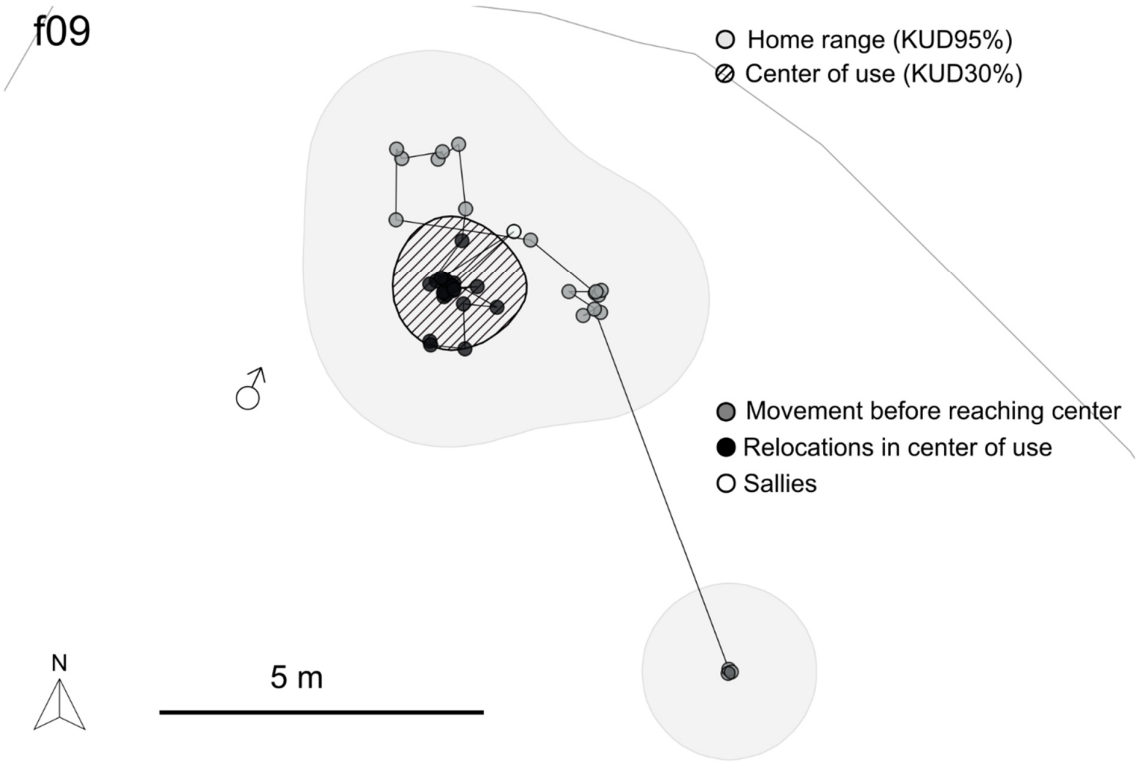
Supplementary Figure 2: Trajectory of female f05. Female trajectory with 1 center of use. The center of use is striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Relocalization points after tagging before reaching a center of use are shown in dark grey. Datapoints in the center of use are indicated in black, sallies to the surrounding are marked with hollow dots, pre-mating movement is indicated with red and post-mating movement until the next center of use is reached with blue dots. The egg deposition site is indicated by a yellow star. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol. This female was tracked for 16 days.



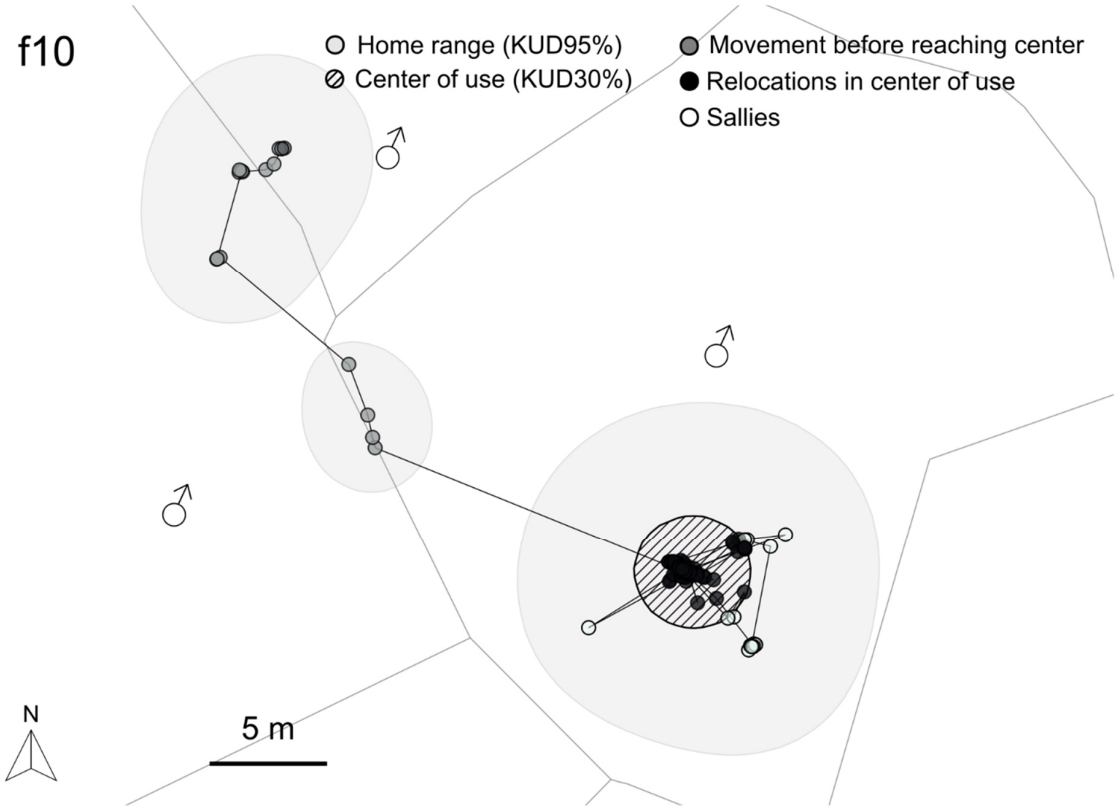
Supplementary Figure 3: Trajectory of female f06. Female trajectory with 1 center of use. The center of use is striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Relocalization points after tagging before reaching a center of use are shown in dark grey. Datapoints in the center of use are indicated in black, sallies to the surrounding are marked with hollow dots, pre-mating movement is indicated with red and post-mating movement until the next center of use is reached with blue dots. The egg deposition site is indicated by a yellow star. This female was observed transporting one tadpole, as indicated with green datapoints. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol. This female was tracked for 16 days.



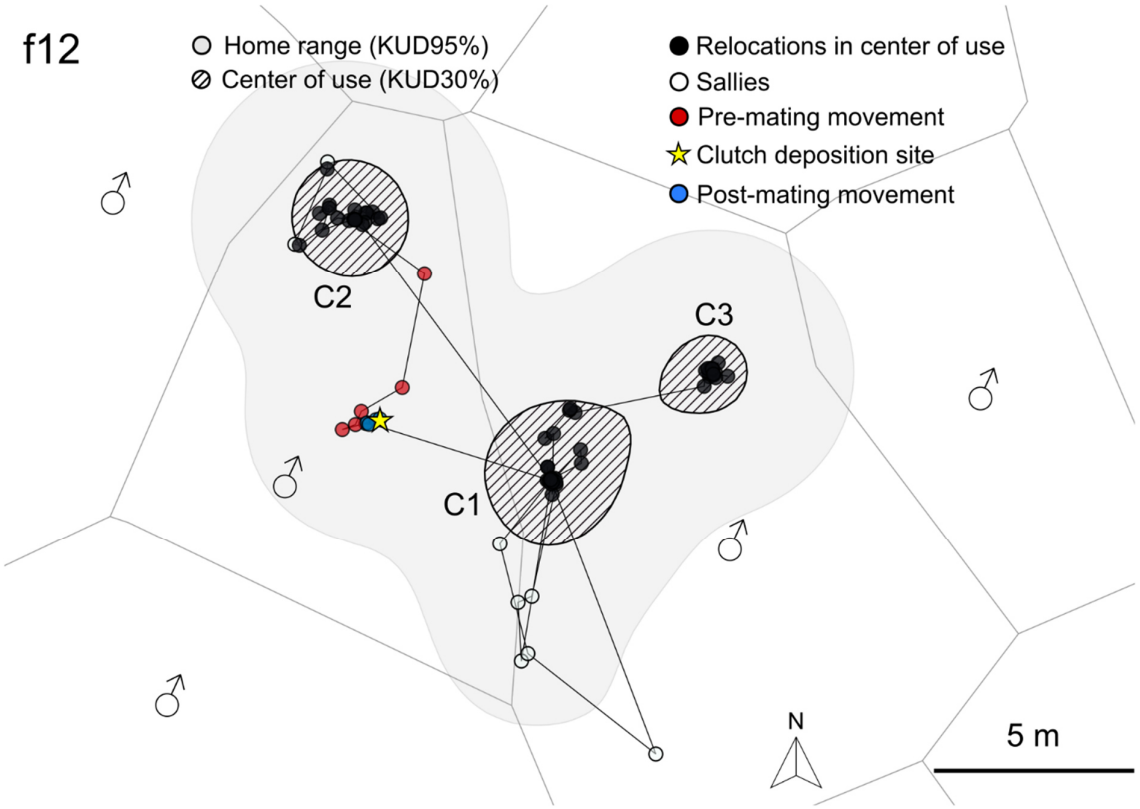
Supplementary Figure 4: Trajectory of female f08. Female trajectory with 1 center of use. The center of use is striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Relocalization points after tagging before reaching a center of use are shown in dark grey. Datapoints in the center of use are indicated in black, sallies to the surrounding are marked with hollow dots. No courtship/mating event was observed for this female. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol. This female was tracked for 7 days.



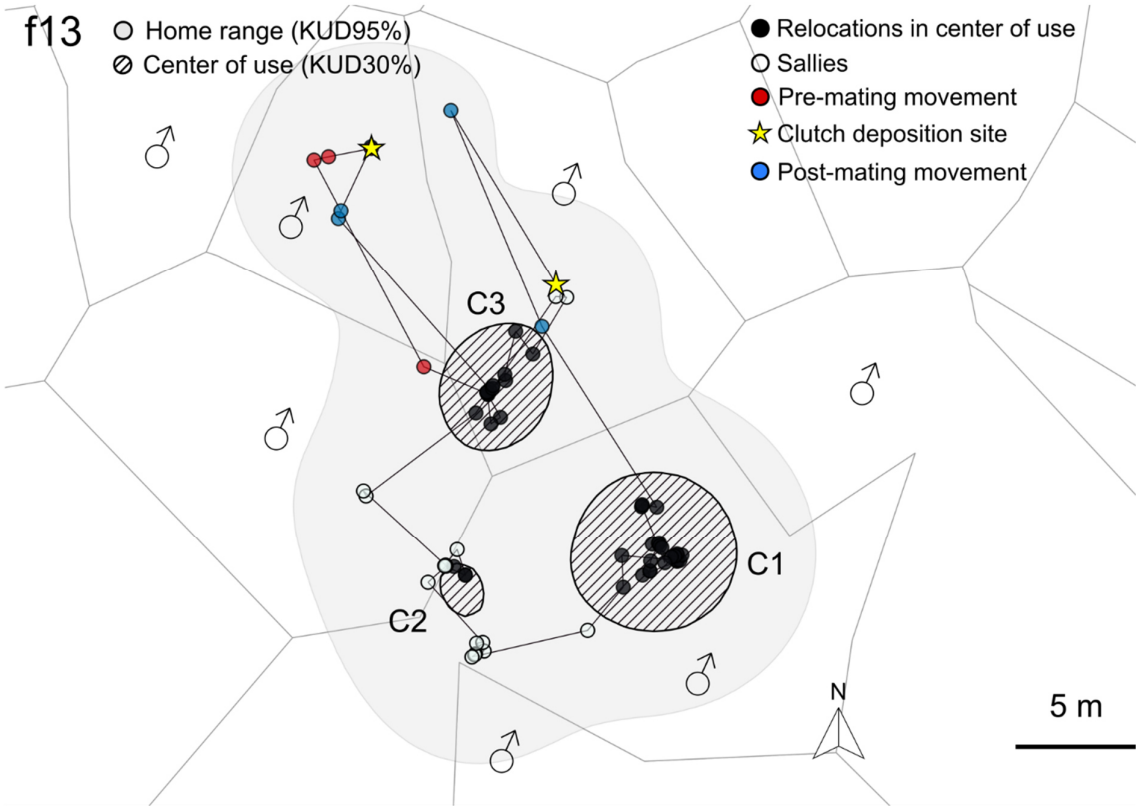
Supplementary Figure 5: Trajectory of female f09. Female trajectory with 1 center of use. The center of use is striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Relocalization points after tagging before reaching a center of use are shown in dark grey. Datapoints in the center of use are indicated in black, sallies to the surrounding are marked with hollow dots. No courtship/mating event was observed for this female. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol. This female was tracked for 6 days.



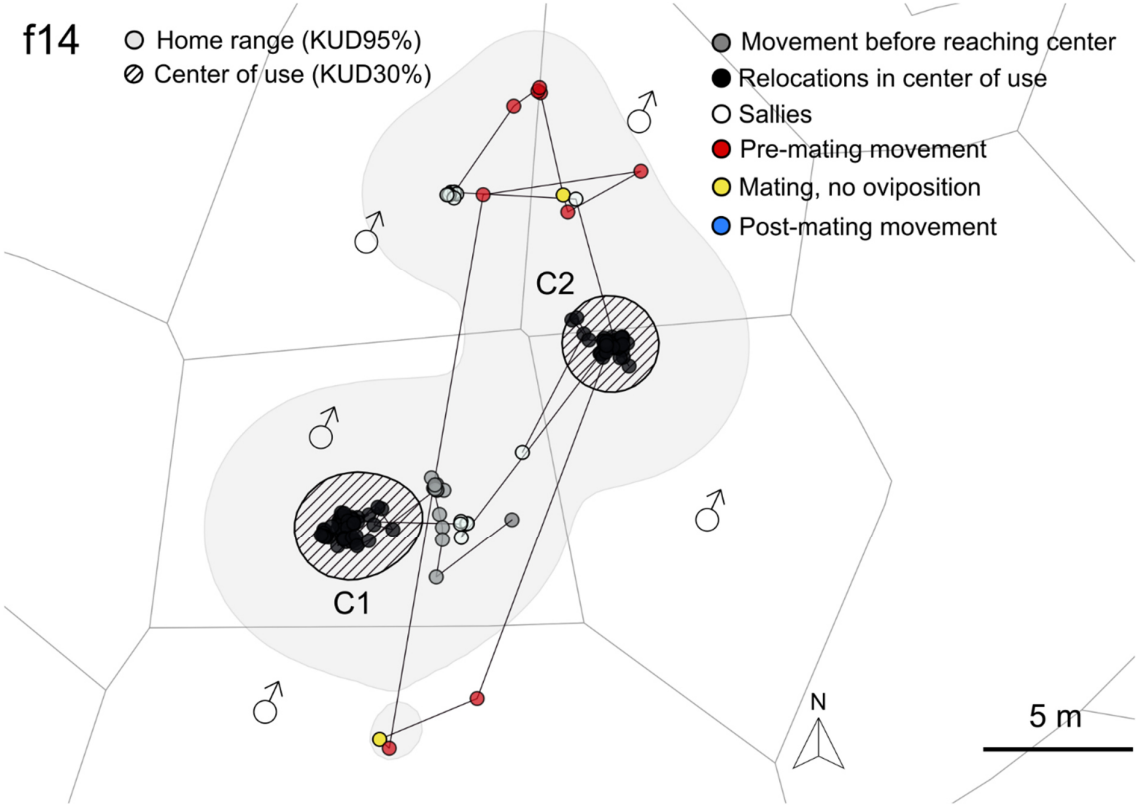
Supplementary Figure 6: Trajectory of female f10. Female trajectory with 1 center of use. The center of use is striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Relocalization points after tagging before reaching a center of use are shown in dark grey. Datapoints in the center of use are indicated in black, sallies to the surrounding are marked with hollow dots. No courtship/mating event was observed for this female. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol. This female was tracked for 13 days.



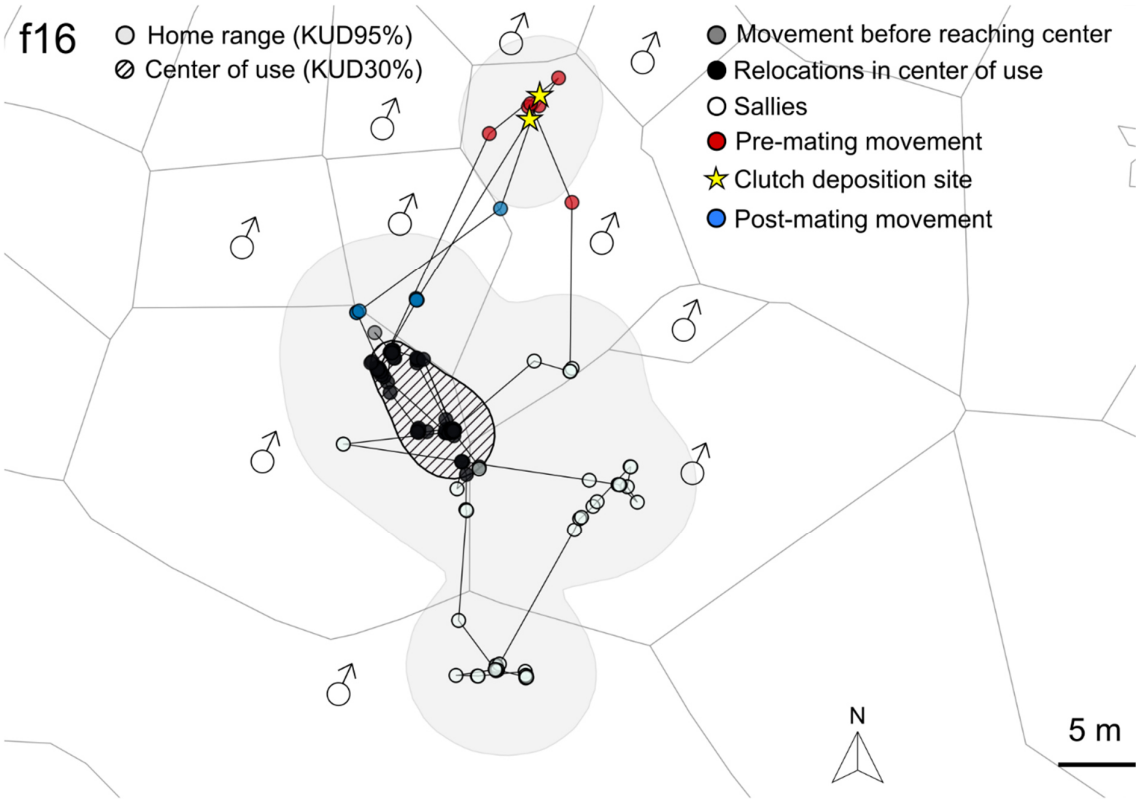
Supplementary Figure 7: Trajectory of female f12. Female trajectory with 3 centers of use. Centers of use (C1, C2, C3) are striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Datapoints in the center of use are indicated in black, sallies to the surrounding are marked with hollow dots, pre-mating movement is indicated with red and post-mating movement until the next center of use is reached with blue dots. The egg deposition site is indicated by a yellow star. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol. This female was tracked for 10 days.



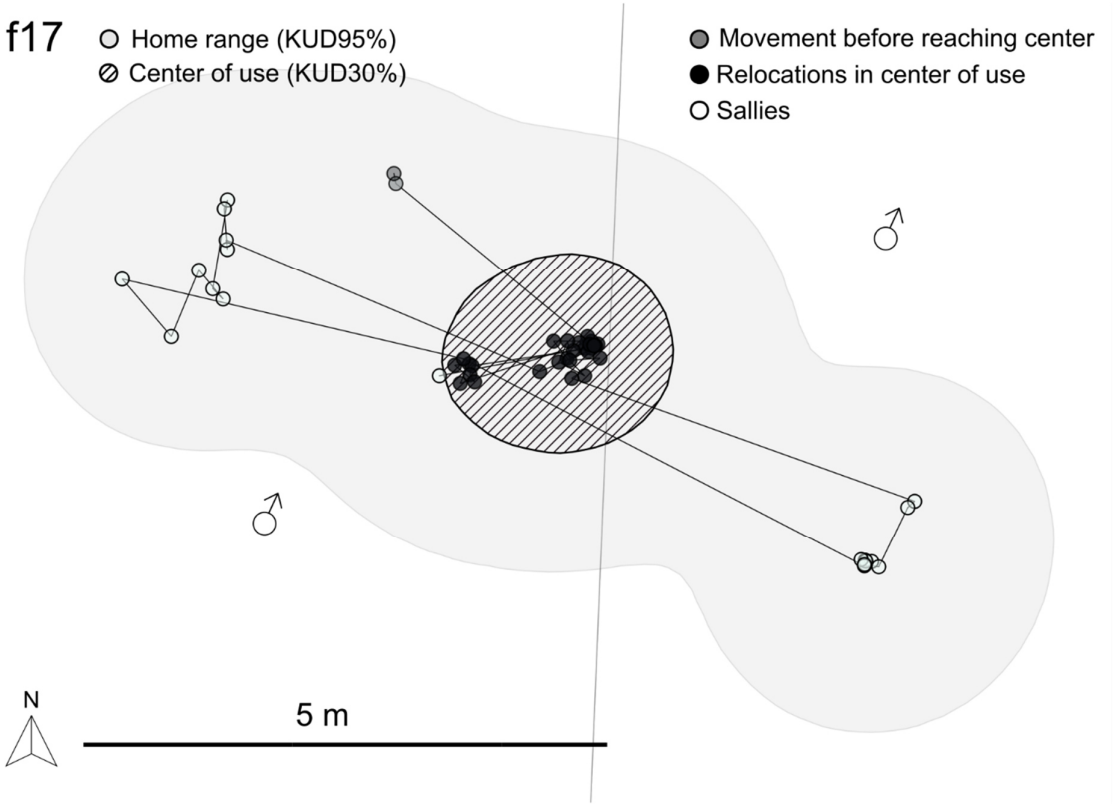
Supplementary Figure 8: Trajectory of female f13. Female trajectory with 3 centers of use. Centers of use (C1, C2, C3) are striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Datapoints in the center of use are indicated in black, sallies to the surrounding are marked with hollow dots, pre-mating movement is indicated with red and post-mating movement until the next center of use is reached with blue dots. The egg deposition site is indicated by a yellow star. This female was tagged after oviposition. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol. This female was tracked for 8 days.



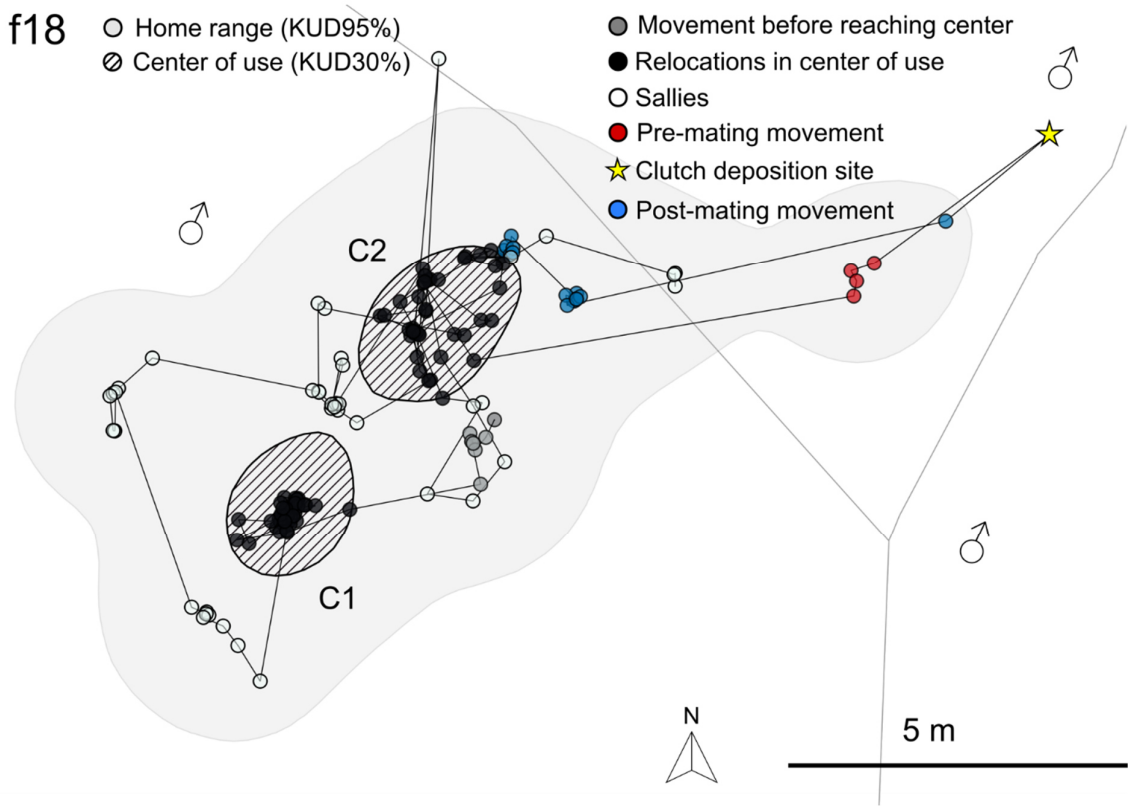
Supplementary Figure 9: Trajectory of female f14. Female trajectory with 2 centers of use. Centers of use (C1, C2) are striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Relocalization points after tagging before reaching a center of use are shown in dark grey. Datapoints in the center of use are indicated in black, sallies to the surrounding are marked with hollow dots, pre-mating movement is indicated with red and post-mating movement until the next center of use is reached with blue dots. The mating site is indicated by a yellow point. This female was detagged after we observed two consecutive courtship/mating events without successful clutch deposition. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol. This female was tracked for 17 days.



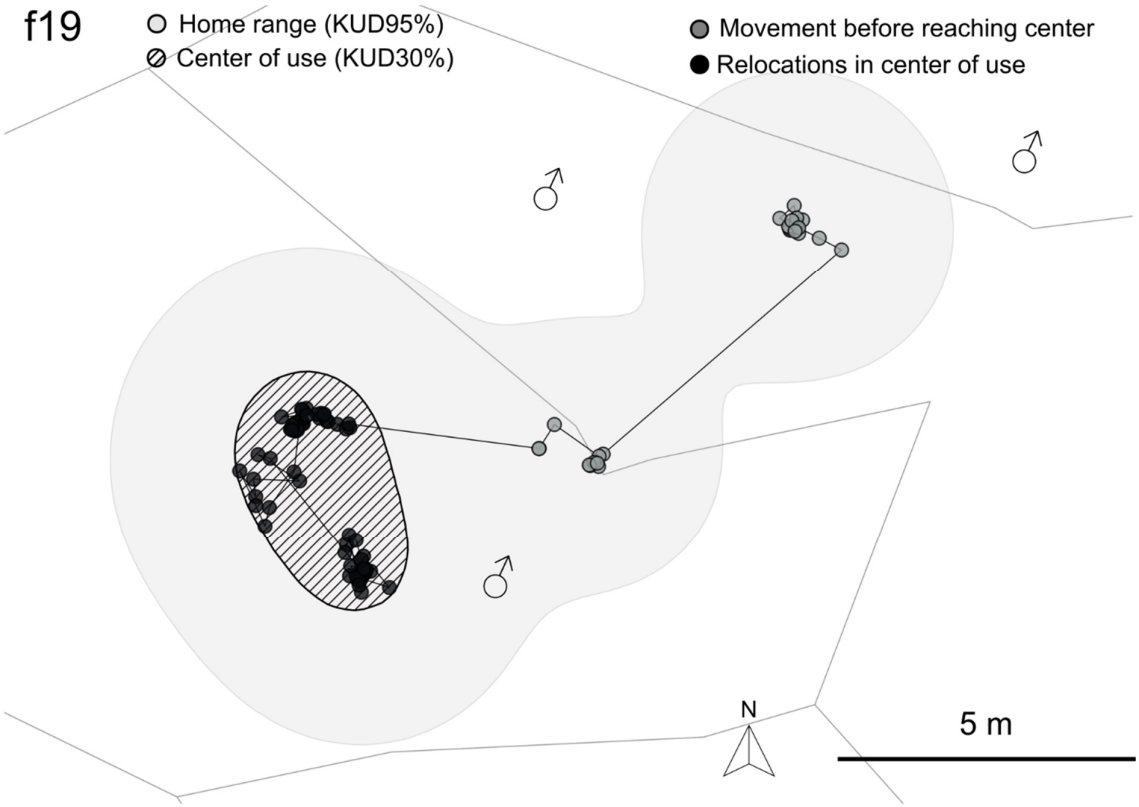
Supplementary Figure 10: Trajectory of female f16. Female trajectory with 1 center of use. The center of use is striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Relocalization points after tagging before reaching a center of use are shown in dark grey. Datapoints in the center of use are indicated in black, sallies to the surrounding are marked with hollow dots, pre-mating movement is indicated with red and post-mating movement until the next center of use is reached with blue dots. The egg deposition site is indicated by a yellow star. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol. This female was tracked for 17 days.



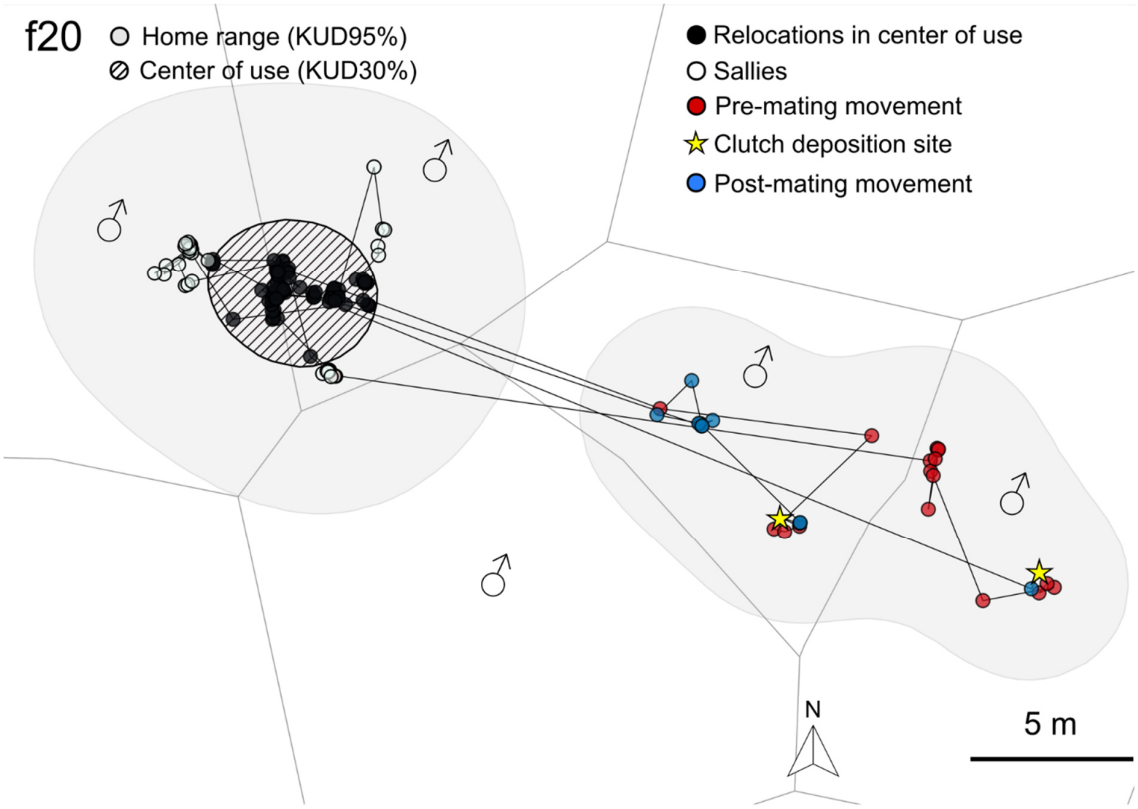
Supplementary Figure 11: Trajectory of female f17. Female trajectory with 1 center of use. The center of use is striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Relocalization points after tagging before reaching a center of use are shown in dark grey. Datapoints in the center of use are indicated in black, sallies to the surrounding are marked with hollow dots. No courtship/mating event was observed for this female. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol. This female was tracked for 7 days.



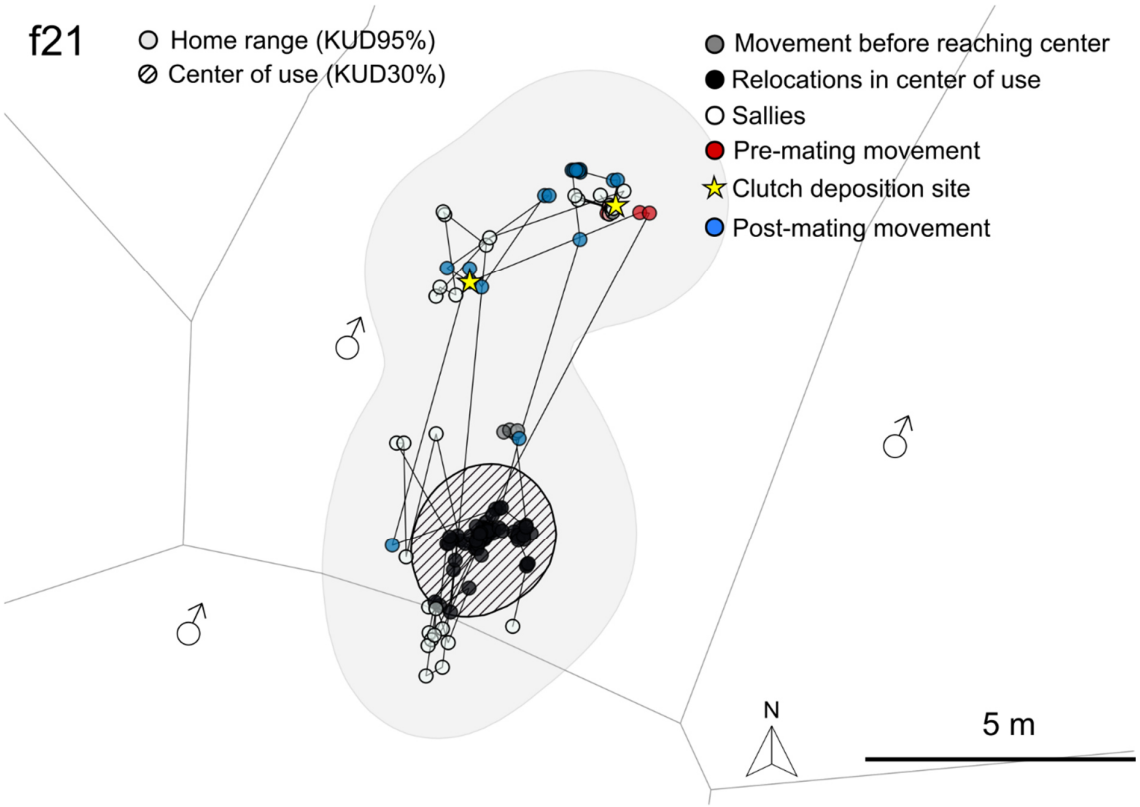
Supplementary Figure 12: Trajectory of female f18. Female trajectory with 2 centers of use. Centers of use (C1, C2) are striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Relocalization points after tagging before reaching a center of use are shown in dark grey. Datapoints in the center of use are indicated in black, sallies to the surrounding are marked with hollow dots, pre-mating movement is indicated with red and post-mating movement until the next center of use is reached with blue dots. The egg deposition site is indicated by a yellow star. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol. This female was tracked for 16 days.



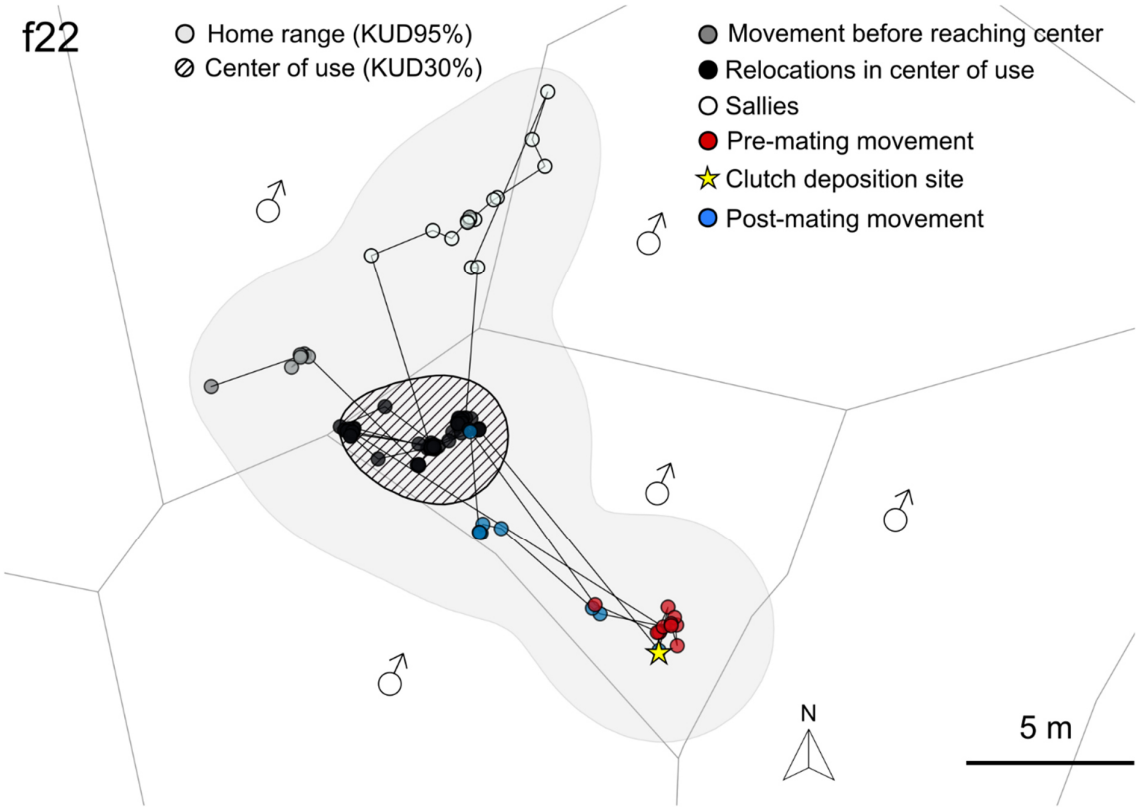
Supplementary Figure 13: Trajectory of female f19. Female trajectory with 1 center of use. The center of use is striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Relocalization points after tagging before reaching a center of use are shown in dark grey. Datapoints in the center of use are indicated in black. No sallies or courtship/mating events were observed for this female. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol. This female was tracked for 10 days.



Supplementary Figure 14: Trajectory of female f20. Female trajectory with 1 center of use. The center of use is striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Datapoints in the center of use are indicated in black, sallies to the surrounding are marked with hollow dots, pre-mating movement is indicated with red and post-mating movement until the next center of use is reached with blue dots. The egg deposition site is indicated by a yellow star. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol. This female was tracked for 17 days.



Supplementary Figure 15: Trajectory of female f21. Female trajectory with 1 center of use. The center of use is striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Relocalization points after tagging before reaching a center of use are shown in dark grey. Datapoints in the center of use are indicated in black, sallies to the surrounding are marked with hollow dots, pre-mating movement is indicated with red and post-mating movement until the next center of use is reached with blue dots. The egg deposition site is indicated by a yellow star. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol. This female was tracked for 14 days.



Supplementary Figure 16: Trajectory of female f22. Female trajectory with 1 center of use. The center of use is striped (KernelUD30). Home range area (KernelUD95) is shaded light grey. Relocalization points after tagging before reaching a center of use are shown in dark grey. Datapoints in the center of use are indicated in black, sallies to the surrounding are marked with hollow dots, pre-mating movement is indicated with red and post-mating movement until the next center of use is reached with blue dots. The egg deposition site is indicated by a yellow star. Territories of surrounding males were estimated with the Voronoi approach and marked with a marssymbol. This female was tracked for 10 days.

ZUSAMMENFASSUNG

Spektakuläre Phänomene wie die kilometerweite Massenwanderung von Amphibien zu ihren Paarungsgebieten ziehen seit jeher die Aufmerksamkeit von Forschern auf sich. Vergleichsweise wenig Beachtung fanden bislang komplexe Bewegungsmuster auf verhältnismäßig kleinem Raum, wie sie zum Beispiel bei Anuren auftreten, die über längere Zeit standorttreu sind. Neotropische Pfeilgiftfrösche (Dendrobatidae) fallen unter diese Kategorie und sind insbesondere für die Komplexität und Diversität ihres Fortpflanzungs- und Brutpflege-Verhalten bekannt. Um kleinräumige Bewegungsabläufe zu untersuchen müssen Methoden angewendet werden, die eine ausreichende spatio-temporale Auflösung zulassen, ohne das Verhalten der Tiere wesentlich zu beeinträchtigen. In dieser Studie bedienen wir uns der Telemetrie um erstmals die Raumnutzung von optisch und verhaltensmäßig unauffälligen Weibchen des gut untersuchten Goldschenkel Baumsteigers (*Allobates femoralis*, BOULENGER 1883) aufzuzeigen. Wir haben insgesamt 17 Weibchen der promiskuitiven Frösche besendert und über Zeiträume zwischen 6 und 17 Tagen untertags jede Stunde lokalisiert. Die Tiere bewegten sich durchschnittlich 1 m pro Stunde, wobei Spitzengeschwindigkeiten von bis zu ~ 24 m pro Stunde an Paarungstagen erreicht wurden. Die zurückgelegten Distanzen sowie das stündliche Aktivitätsmuster der Weibchen unterschieden sich erheblich zwischen Tagen mit Balz- bzw. Paarungsverhalten und Tagen ohne reproduktivem Verhalten. An kühleren und regenreichen Tagen bewegten sich die Frösche generell mehr, das Paarungsverhalten war mit maßgeblich erhöhten Wegstrecken assoziiert. Die Größe der Streifgebiete von *A. femoralis* Weibchen nach 14 Tagen variierte zwischen 24.8 m^2 und 285.2 m^2, wobei ca. 30% dieses Revieres auf Balz- und Paarungs-assoziierte Raumnutzung entfiel. Die Frösche verbrachten ~62% ihrer Zeit in ein bis drei kleineren Aktivitäts-Zentren mit einer Größe von 2.5 m^2 bis 66 m^2. Wir haben im Zuge des Trackings 21 Balzereignisse beobachtet, von denen 19 mit einer Eiablage endeten. Für sieben Weibchen konnten je 2 aufeinanderfolgende Eiablagen beobachtet werden. Die durchschnittliche Zeit von 8 Tagen zwischen 2 Eiablagen sowie die Gelegegröße von ~17.5 Eiern bestätigen erstmals Weygolds (1980) Beobachtungen von Tieren in Gefangenschaft in einer natürlichen Population. *A. femoralis* Weibchen passten weder ihre Raumnutzung noch ihr Zeitmanagement an die Dichte der Männchen in ihrer Umgebung an. Ebenso konnten wir kein weitläufiges exploratives Verhalten oder Überwachung alter Gelege beobachten. Unsere Studie zeigt beispielhaft wie die Wissenslücke über detaillierte Bewegungsmuster und Zeitaufteilung bei Pfeilgiftfröschen mit Hilfe von Telemetrie geschlossen werden kann.