

Relying on known or exploring for new? Movement patterns and reproductive resource use in a tadpole-transporting frog

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Animals relying on uncertain, ephemeral and patchy resources have to regularly update information about profitable sites. For many tropical amphibians, widespread, scattered breeding pools constitute such fluctuating resources. Among tropical amphibians, poison frogs (Dendrobatidae) exhibit some of the most complex spatial and parental behaviors – including territoriality and tadpole transport from terrestrial clutches to ephemeral aquatic deposition sites. Recent studies have revealed that poison frogs rely on spatial memory to successfully navigate through their environment. This raises the question of when and how these frogs gain information about the area and suitable reproductive resources. To investigate the spatial patterns of pool use and to reveal potential explorative behavior, we used telemetry to follow males of the territorial dendrobatid frog *Allobates femoralis* during tadpole transport and subsequent homing. To elicit exploration, we reduced resource availability experimentally by simulating desiccated deposition sites. We found that tadpole transport is strongly directed towards known deposition sites and that frogs take similar direct paths when returning to their home territory. Frogs move faster during tadpole transport than when homing after the deposition, which probably reflects different risks and costs during these two phases of movement. We found no evidence for exploration, neither during transport nor homing, and independent of the availability of deposition sites. We suggest that prospecting during tadpole transport is too risky for the transported offspring as well as for the transporting male. Relying on spatial memory of multiple previously discovered pools appears to be the predominant and successful strategy for the exploitation of reproductive resources in *A. femoralis*. Our study provides for the first time a detailed description of poison frog movement patterns during tadpole transport and corroborates recent findings on the significance of spatial memory in poison frogs. When these frogs explore and discover new reproductive resources remains

unknown.

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22 Abstract

23

24 Animals relying on uncertain, ephemeral and patchy resources have to regularly update
25 information about profitable sites. For many tropical amphibians, widespread, scattered breeding
26 pools constitute such fluctuating resources. Among tropical amphibians, poison frogs
27 (Dendrobatidae) exhibit some of the most complex spatial and parental behaviors – including
28 territoriality and tadpole transport from terrestrial clutches to ephemeral aquatic deposition sites.
29 Recent studies have revealed that poison frogs rely on spatial memory to successfully navigate
30 through their environment. This raises the question of when and how these frogs gain
31 information about the area and suitable reproductive resources. To investigate the spatial patterns
32 of pool use and to reveal potential explorative behavior, we used telemetry to follow males of the
33 territorial dendrobatid frog *Allobates femoralis* during tadpole transport and subsequent homing.
34 To elicit exploration, we reduced resource availability experimentally by simulating desiccated
35 deposition sites.

36 We found that tadpole transport is strongly directed towards known deposition sites and that
37 frogs take similar direct paths when returning to their home territory. Frogs move faster during
38 tadpole transport than when homing after the deposition, which probably reflects different risks
39 and costs during these two phases of movement. We found no evidence for exploration, neither
40 during transport nor homing, and independent of the availability of deposition sites. We suggest
41 that prospecting during tadpole transport is too risky for the transported offspring as well as for
42 the transporting male. Relying on spatial memory of multiple previously discovered pools
43 appears to be the predominant and successful strategy for the exploitation of reproductive
44 resources in *A. femoralis*. Our study provides for the first time a detailed description of poison

45 frog movement patterns during tadpole transport and corroborates recent findings on the
46 significance of spatial memory in poison frogs. When these frogs explore and discover new
47 reproductive resources remains unknown.

48

49 **Introduction**

50 In a dynamic environment resource availability changes in time and space, which has major
51 influences on animal movement decisions (Milner-Gulland, Fryxell & Sinclair, 2011; Bell,
52 2012). Animals that rely on unpredictable, ephemeral, and patchy resources have to explore their
53 environment regularly (Roshier, Doerr & Doerr, 2008). Updating information on profitable
54 resources can be achieved by exploring unknown areas to collect new information, by frequently
55 visiting already known patches to affirm the availability of resources or by prospecting for new
56 resources within familiar areas (Real, 1981; Eliassen et al., 2009; Díaz et al., 2013). However,
57 exploration comes at a cost of the time spent searching, which conflicts with other fitness-related
58 activities such as territory defense (Ydenberg & Krebs, 1987) and advertising for mates (Kaefer
59 et al., 2012). Exploration also increases the exposure to sit-and-wait predators and thus overall
60 predation risk (Stamps, 1995). Thus, animals depending on fluctuating resources need to find a
61 balance between relying on known resources and prospecting for new ones (Milner-Gulland,
62 Fryxell & Sinclair, 2011).

63 Most amphibians depend on aquatic sites for breeding, making them particularly suitable for
64 investigating, how animals deal with varying availability, stability and distribution of resources.
65 Amphibians exhibit a vast diversity of reproductive strategies ranging from explosive breeders
66 that gather in large ponds for synchronized spawning, to prolonged breeders with terrestrials
67 clutches that use small widespread pools for tadpole development (Duellman & Trueb, 1994;

68 Crump, 2015). Tropical amphibians, in particular, are renowned for the variety of aquatic sites
69 used for reproduction (Wells, 2007). Despite the overall high amount of rainfall, seasonal
70 variability can have a strong impact on the availability of breeding resources and thus on the
71 reproductive success of tropical amphibians (Aichinger, 1987; Bertoluci & Rodrigues, 2002;
72 Gottsberger & Gruber, 2004). During periods of heavy rainfall, potential breeding sites such as
73 small pools in the ground can appear within hours. However, due to the high environmental
74 temperatures also desiccation can happen rapidly, even during the rainy season. To date, it
75 remains mostly unknown how tropical amphibians deal with the uncertainty of breeding sites,
76 and which mechanisms they use to find these scattered resources.

77 The Neotropical poison frogs (Dendrobatidae) exhibit a variety of complex spatial behaviors
78 such as territoriality, tadpole transport, and offspring provisioning (Weygoldt, 1987; Pröhl, 2005;
79 Lötters, 2007). Most poison frogs shuttle their larvae from terrestrial clutches to widespread,
80 ephemeral deposition sites, where the larvae complete their development. While complex
81 parental behavior in this group of frogs has attracted a considerable amount of research (for
82 review, Wells, 2007), the associated movement patterns associated and the factors shaping them
83 have hardly been quantified and remain poorly understood. When transporting their offspring,
84 frogs need to know when and where to go for suitable water bodies that are sufficiently persistent
85 to allow larval development, but ephemeral enough to minimize predator abundance (c.f.
86 Murphy, 2003; Lehtinen, 2004). Recent studies have shown that poison frogs can use flexible
87 learning strategies in spatial tasks in captivity (*Dendrobates auratus*, (Liu et al., 2016)), rely on
88 experience for successful homing after translocation (*Allobates femoralis*, (Pašukonis et al.,
89 2013, 2014a)) and for finding tadpole deposition sites in the field (Pašukonis et al., 2016).
90 Together these results suggest that poison frogs rely on spatial memory to successfully navigate

91 in their environment, which raises the question of when and how these frogs gain information
92 about the area and in particular how they update information on the availability of their
93 reproductive resources. To date, exploratory behavior has only been reported in one poison frog
94 species (*Dendrobates auratus*, (Summers, 1989)) as prospecting trips after tadpole deposition
95 and between tadpole transport events. However, this study did not quantify the associated
96 movements, and in general little is known about the movement patterns during tadpole transport
97 in poison frogs.

98 *Allobates femoralis* is a small territorial poison frog with predominantly male tadpole transport.
99 Males use multiple, scattered aquatic sites outside their territories, which is suggested to increase
100 offspring survival (Ringler et al., 2013; Erich et al., 2015). Dependency on unpredictable
101 resources and experience-based navigation render *A. femoralis* an ideal study species to address
102 questions on mechanisms and timing of environmental exploration and learning. The
103 demonstrated ability of *A. femoralis* to navigate to small goals via a direct path (Pašukonis et al.,
104 2014a,b, 2016) facilitates the interpretation of movement patterns, as it suggests that non-
105 directed movement in the local area is rather exploratory behavior than an inability to self-
106 orientate. Since tadpole transport constitutes the most prominent long-distance movement in *A.*
107 *femoralis* (Ringler, Ursprung & Hödl, 2009; Ringler et al., 2013) it has been postulated that the
108 frogs update their knowledge about the area by exploring during tadpole transport and
109 subsequent homing (Pašukonis et al., 2013, 2014b). In addition, the longest observed tadpole
110 transports correspond to the farthest distances where territorial males still show high homing
111 success after translocations (approx. 200m, Pašukonis et al., 2013; Ringler et al., 2013) – further
112 suggesting a link between tadpole transport and spatial learning.

113 Exploration during tadpole transport would allow gaining information about new and altered
114 resources, but it would also increase costs. During the breeding season male *A. femoralis* are
115 mostly found in their territories, calling to attract females and to repel competing males (Kaefer
116 et al., 2012). Leaving the territory and prolonged movement would increase the risk of losing
117 mating opportunities, losing the entire territory, and can increase the risk of predation (e.g,
118 Roithmair, 1992; Amézquita et al., 2009) and energetic expenditure. Tadpole transport consists
119 of two phases: shuttling of tadpoles until deposition, and homing back to the territory.
120 Exploratory behavior on the way to known deposition sites would also involve potential costs for
121 the offspring being transported, such as increased risk of desiccation (Downie et al., 2005),
122 whereas during homing it would only involve costs for the male. Thus, the net benefit of
123 prospecting for new deposition sites during homing should be higher, which might be reflected
124 in frog movement patterns.

125 In this study we quantified the movement patterns of tadpole transport, determined potential
126 factors influencing them (i.e., odor cues and weather), and examined whether frogs perform any
127 exploratory behavior. We attempted to induce exploratory behavior by removing artificial pools
128 and thus experimentally simulating desiccation of reproductive resources. We followed
129 transporting male *A. femoralis* towards artificial deposition sites and back to the territory using
130 telemetry. We expected tadpole carriers to show fast, directional movement to known pools, as
131 they should aim to reduce potential costs for the offspring being transported and rather perform
132 exploratory detours on the way back to their territories. Further, we expected frogs encountering
133 a removed pool before deposition to be more likely to perform exploratory detours and to
134 continue visiting other deposition sites to update the information on pool availability.

135

136 **Materials & Methods**

137 Study species and area

138 *Allobates femoralis* is a small diurnal frog (snout-urostyle length approximately 25 mm)
139 common throughout Amazonia and the Guiana Shield (Amézquita et al., 2009). During the rainy
140 season males occupy territories which they advertise by calling and defend for up to several
141 months (Roithmair, 1992; Ringler, Ursprung & Hödl, 2009). Mating and oviposition of
142 approximately 20 eggs take place in the leaf litter inside the male's territory (Roithmair, 1992;
143 Ringler et al., 2012). After 15-20 days of development, the male allows the tadpoles to wriggle
144 on his back and transports them to multiple, widely distributed deposition sites (Ringler et al.,
145 2013; Erich et al., 2015). Females will transport the offspring only in cases where males
146 disappear (Ringler et al., 2015). For tadpole deposition frogs use a variety of small to medium
147 sized terrestrial water bodies such as rain-flooded depressions, holes in fallen trees, or palm
148 bracts. Aquatic deposition sites constitute a limiting resource for *A. femoralis*, and frogs readily
149 use artificial pools if provided in their natural habitat (Ringler, Hödl & Ringler, 2015).

150 We carried out the study from 18 January–12 March 2015 in a lowland rainforest on a 5 hectare
151 river island near the “Camp Pararé” field site at the CNRS “Nouragues Ecological Research
152 Station” in the Nature Reserve “Les Nouragues”, French Guiana (3°59'N, 52°35'W) (Bongers et
153 al., 2013; Ringler et al., 2016). All necessary permissions were provided by the Centre National
154 de la Recherche Scientifique (CNRS) and by the Direction Régionale de l'Environnement, de
155 l'Aménagement et du Logement (DEAL: ARRETE n°2011-44/DEAL/SMNBSP/BSP). The
156 island population was established by introducing 1800 genotyped *A. femoralis* tadpoles from a
157 nearby population in 2012 (Ringler, Mangione & Ringler, 2014) and released in artificial pools
158 (volume ~15 l, inter-pool distance ~10 m). In 2013, the pools were rearranged in a cross-shaped

159 array of 13 pools (inter-pool distance ~20 m). At the beginning of our study in 2015 we removed
160 every second pool to experimentally simulate dried up water bodies, leaving 8 pools available.
161 Occasionally, tadpole carriers also used natural deposition sites such as small flooded
162 depressions and burrows on the forest floor. In total, we recorded four such natural sites which
163 ephemerally filled with water, depending on the weather conditions, and which were visited by
164 tadpole transporting frogs during our study (Fig.1).

165

166 Territory sampling

167 To determine male territories, we continuously scanned the area for calling males during our
168 study. All frogs were caught with transparent plastic bags, photographed and individually
169 identified by their unique ventral coloration pattern (Ringler, Mangione & Ringler, 2014) using
170 the pattern matching software Wild-ID (Bolger et al., 2011). We determined sex based on calling
171 and the presence (male) or absence (female) of a vocal sac. We recorded exact capture positions
172 on a detailed GIS background map (Ringler et al., 2016) using tablet PCs (WinTab 8, Odys) with
173 a mobile GIS software (ArcPad 10, ESRI). To calculate the territory center for each male, we
174 only used data points where males displayed territorial behavior (calling, courtship, aggressive
175 approach).

176

177 Tadpole carrier tracking

178 To sample tadpole carriers, we visually scanned the area around each pool (approx.: 2 m radius)
179 every day between 0700–1300 h as tadpole transport mainly occurs during the morning
180 (Aichinger, 1987; Ringler et al., 2013). We caught the tadpole carriers with transparent plastic

181 bags, photographed them for identification, and recorded their exact position on the GIS map.
182 We counted the number of transported tadpoles, and in cases where some tadpoles fell off during
183 catching and handling, we returned them to the male's back.
184 Before the release, we equipped transporting males with a transponder using a waistband (Fig.
185 S1). The entire procedure took a few minutes and did not disrupt tadpole transport or deposition
186 behavior regardless of whether the tadpoles were manipulated or not. We followed tagged
187 tadpole carriers using the harmonic direction-finding (HDF) telemetry technique. This system
188 consists of a passive reflector/transponder, which is attached to the animal and an active
189 directional transceiver, which emits and then receives the reflected radio signal. It allows to track
190 smaller animals than conventional active radio tracking (Mascanzoni & Wallin, 1986; Rowley &
191 Alford, 2007) and it has been successfully used in *A. femoralis* (Pašukonis et al., 2014a,b). We
192 fitted the tags using a 2 mm diameter silicon tube, forming a waistband with an additional strap
193 between the hind legs to prevent the tag from rotating. Both parts were fixed with a cotton
194 thread, which would break and release the waistband after approximately two to three weeks
195 (personal observation KB, AP) in case an individual was not recaptured. The waistbands carried
196 a small diode beneath a color-coded sealing and a T-shaped dipole antenna made of flexible
197 coated wire. The long end (~12 cm) of the antenna was freely dragging behind the moving frog
198 while the short end (~2 cm) was secured inside the waistband. As *A. femoralis* is strictly diurnal,
199 we only tracked frogs during daylight hours (0700–1900 h), relocating each individual and
200 recording their position every 30–60 min. We followed each frog until all tadpoles had been
201 deposited and the male had returned to his territory, where the tag was removed. Frogs were
202 assumed to have returned when they approached previous encounter locations where they had
203 shown territorial behavior. During tracking we tried to minimize disturbances by carefully

204 approaching the signal source while searching with the transceiver until the frog was visually
205 spotted or the origin of the signal could be narrowed down to less than 1 m. During tracking, we
206 approached individual frogs from varying directions not to influence and bias the movement in a
207 specific direction. As *A. femoralis* responds to disturbance rather by hiding than by directed
208 escape movements we assume that occasional disturbances had a negligible influence on the
209 directionality of long distance movements. We caught tagged individuals when they had not
210 moved for more than a day to check for tentative issues such as skin injuries – in a single case we
211 immediately removed the tag. In one case without movement for more than two days but without
212 apparent injuries we also removed the tag to minimize any potential long-term effects on
213 behavior.

214

215 Movement analysis

216 We handled and visualized spatial data in the GIS software ArcGIS10 (ESRI) after projecting
217 (UTM-zone 22N, WGS1984), and all analyses were performed in the statistical software R
218 version 3.2.0 (Team, 2014). We split the full trajectories of tracked frogs into tadpole transport
219 (TT), from the first encounter point to the last deposition site, and homing trajectories (HT), from
220 the last deposition site back to the home territory. Movement distance, duration, and speed were
221 calculated for each TT and HT. For individuals, which took more than one day to complete
222 deposition and/or homing, we excluded the nights (-12 h per night) to estimate the average time a
223 frog was moving during tadpole transport. In most cases, the observed TT did not cover the full
224 TT as the frogs were encountered on their way to the pools or in the close vicinity of them. We
225 excluded individuals encountered immediately before tadpole deposition (frogs already present
226 at a pool or less than 2 tracking locations before reaching the pool) from the analysis of TT

227 trajectories. We interpolated the total distances of TTs by approximating the missing part from
228 the territory center until the first encounter location by a straight-line to obtain minimum distance
229 estimates (see Fig. 2).

230 We created a generalized linear mixed model (GLMM) to test the effects of tadpole presence
231 (TT vs. HT) on the movement speed of frogs (family = gamma, link = logit). As response
232 variable, we used the average speed per TT and HT, as explanatory variable “tadpoles present”
233 (yes/no), and individual frog ID as random factor to account for repeated trajectories of the same
234 individuals. Since frog activity varies throughout the day and depends on weather conditions
235 (Bellis, 1962; Brooke, Alford & Schwarzkopf, 2000), we investigated potential effects of
236 weather on the frogs’ movement speed using temperature and rainfall measurements, both from
237 an above-canopy weather station (Nourflux: rainfall sensor Campbell ARG100, temperature
238 sensor Vaisala HMP155A). In contrast to the previous model, where the focus was on certain
239 trajectory sections (TT and HT), we here focused on 3 h intervals to investigate variations in the
240 frogs’ activity (here: movement speed). The 3 h intervals represent four potentially different
241 daily activity periods in *A. femoralis*, with tadpole transport happening predominately in the
242 morning, low activity around noon, high calling activity during the afternoon, and high calling
243 activity and most female-male interactions (e.g., courtship) in the evening (personal observation
244 by all authors; see also (Kaefer et al., 2012; Ringler et al., 2013)). We used a GLMM (family =
245 gamma, link = logit), with speed as response variable, and the explanatory variables “tadpoles
246 present” (yes/no), “time of the day” (split in four 3 h intervals: 0700-1000, 1000-1300, 1300-
247 1600, 1600-1900 h), average “temperature” for each corresponding interval, and cumulative
248 “rain” in millimeters during each interval. Since this analysis is not within the main focus of this
249 study, we present the results in the supplemental information (Table S1, S2).

250

251 Pool visits

252 We defined “pool visit” as frogs actually entering a potential deposition site (either on/in a filled
253 pool or on the removed/dried out pool location). For each tadpole carrier, we recorded all
254 potential tadpole deposition sites visited (available/removed artificial pool or available/dried out
255 natural site), and if tadpole deposition occurred at available pools or not. To test whether frogs
256 explore further pools after the complete deposition of their offspring, we recorded for each
257 location whether tadpoles were still present on the males back or not. If frogs moved to further
258 pools without tadpoles on their back, we would have considered this as exploratory behavior. In
259 addition, we calculated the average number of deposition sites frogs visited (available/removed
260 artificial pool or available/dried out natural site) per tadpole transport. We excluded trajectories
261 with only one final deposition site and no detailed TT. To assess whether frogs usually choose
262 the closest pool to their territory, we compared the distances from the respective territory centers
263 to the first pool a male visited to the distance to the nearest pool site (all natural and artificial
264 deposition sites were taken into account, regardless of whether sites were available or not).

265

266 Movement precision

267 To investigate whether frogs explore the surrounding area by taking additional detours, we
268 estimated the precision of the frogs’ orientation towards the upcoming pools during TTs, and
269 towards the territory during the HTs. To estimate navigation precision we calculated three
270 different parameters: (1) the straightness coefficient (SC) of the trajectory, (2) the average
271 angular deviation between the ideal orientation angle and consecutive tracking locations, and (3)
272 the average normal distance of tracking locations from the straight-line path. The SC is defined

273 as the ratio between the straight-line distance to the respective goal and the actual path distance.
274 SC ranges from 0 to 1 with 1 indicating a perfectly straight trajectory. The angular deviations
275 were measured as the absolute angular difference between the ideal direction (angle from each
276 tracking location to the respective goal) compared to the actual direction of the frog's movement
277 (angle from each tracking location to the next one). For the distance from the straight-line path,
278 we calculated the perpendicular deviation of each tracking location from the straight path. While
279 the SC takes into account the entire trajectory at once, the average angular deviations rather
280 describes the movement decisions from location to location, and the distance from the straight-
281 line path assesses the frog's position in relation to the straight line for every location. We
282 calculated the mean angular deviation and distance from the straight-line path by averaging all
283 values per TTs and HTs in order to have three precision measurements per TTs and HTs.
284 We tested for significant goal-directed orientation using absolute angles calculated with the
285 "as.ltraj" function from the package "adehabitatLT" (Calenge, 2015) per TTs and HTs using
286 Rayleigh tests with the package "circular" (Agostinelli & Lund, 2011).
287 In addition, we tested whether the precision during TTs differed (for example resulting from
288 olfactory cues from the water), when tadpole carriers approached an available deposition site
289 (artificial or natural pool) or an unavailable pool site (removed or desiccated). Therefore, we
290 compared the precision of TTs (SC, average angular deviation and average distance from the
291 straight line path per trajectory) of frogs which were heading towards available and non-
292 available pools. We used different GLMMs with the "SC" (family = beta, link = logit), "average
293 angular deviation" (family = gamma, link = logit) and "average distance to the straight-line path"
294 (family = gamma, link = logit) as response variable. For all three models, we used "heading

295 towards an available vs. non-available pool” as explanatory variable and individual frog ID as
296 random effect.

297 Finally, we investigated potential differences in precision along the tracked HTs between frogs
298 that did and did not encounter a site with a non-available pool (removed pools and naturally
299 dried out water bodies) during prior tadpole transport. For the analysis, we used different linear
300 mixed models (LMM), with “average angular deviation” and “average distance from the straight-
301 line path” as response variable and a GLMM (family = beta, link = logit) with “SC” as response
302 variable. For all three models, we used “removed pool encountered during prior tadpole
303 transport” (yes/no) as explanatory variable and the individual frog ID as random factor to
304 account for repeated trajectories of the same individuals.

305

306 Model selection

307 All full models except for one only contained a single explanatory variable, which was a binary
308 factor. We compared these models with the corresponding null (intercept) model based on the
309 second-order form of Akaike’s information criterion (AICc; (Hurvich & Tsai, 1989)). No
310 difference between the full model and the null model (i.e. $\Delta AICc \leq 2$) indicates that the variation
311 of the response variable is not better explained by the full model than by the null model
312 (Burnham & Anderson, 2002). In this case the null hypothesis is supported and we therefore do
313 not present the model parameters in the results. Following the information theoretic approach
314 (Burnham & Anderson, 2002), we created for the model with several explanatory variables all
315 possible candidate models (all-subset modelling). We ranked them according to their AICc
316 values and selected those within $\Delta AICc \leq 2$ with respect to the top-ranked model. We estimated

317 parameters for each explanatory variable included in the $\Delta AICc \leq 2$ subset by model averaging
318 following Burnham and Anderson (Burnham & Anderson, 2002).

319 All models were calculated using the R packages “lme4” (Bates & Maechler, 2010) or
320 “glmmADMB” (Bolker et al., 2014), and for model averaging the package “MuMIn” (Bartoń,
321 2013).

322

323 **Results**

324 Frog sampling and movement analysis

325 During the study period, we captured 67 individual males for a total of 658 times. 408 captures
326 were associated with male territorial behavior and were used to calculate territory centers (Fig.1).
327 We observed 50 tadpole transports by 30 males and tagged 20 individuals to track 28 tadpole
328 transports. From all tagged frogs, we used the TTs and/or HTs of 16 individuals for movement
329 analysis: $n = 15$ TTs from 10 individuals (with five times 2 trajectories per individual); $n = 22$
330 HTs from 16 individuals, (with once 3 trajectories per individual and four times 2 trajectories per
331 individual). Other trajectories were excluded as frogs had not moved further than 5 m for two
332 days ($n = 1$), had an injury ($n = 1$), the entire tadpole transport took place inside the territory ($n =$
333 1) or were depredated by a spider ($n = 1$). All averaged values (i.e., distance, time and speed)
334 were estimated by first averaging per trajectory section (TT and HT), followed by calculating the
335 overall average from all TTs and HTs.

336 Summing up the entire trajectory (interpolated start + TT + HT; $n = 14$, 10 individuals) frogs
337 moved on average 141.73 m (sd = 68.87 m, range = 59.94–276.01 m) and were tracked on
338 average for 17.62 h (sd = 14.01, range = 6.42–58.4 h, nights excluded). Tracked TT ($n = 15$, 10
339 individuals, see Fig. 2) on average covered a distance of 56.34 m (sd = 38.09 m, range = 4.93–

340 141.37 m). The interpolated path was on average 39.21 m (sd = 24.72 m, range = 0–95.16 m, for
341 n = 12, 7 individuals), adding up to an average distance of 87.71 m (sd = 40.29 m, range =
342 35.32–166.43 m) for the whole TT. The time until all tadpoles were deposited was on average
343 5.55 h (sd = 2.7 h, range = 2.08–13.25 h, nights were excluded for n = 1). The speed during
344 tracked TTs was on average 10.16 m/h reaching a maximum of 17.91 m/h (distance = 55.16 m,
345 time = 3.08 h; for further details see Table S3). During HTs, male frogs moved an average
346 distance of 54.57 m (sd = 29.63 m, range = 15.98–123.46 m, n = 22, 16 individuals, see Fig. S2)
347 and the average return time was 10.78 h (sd = 10.38 h, range = 1–49.9 h) until frogs were back in
348 the territory (nights were excluded for n = 10). Speed during homing was on average 7.22 m/h
349 with a maximum of 22.16 m/h (distance = 22.16 m, time = 1 h; for further details see: Table S4).
350 Frogs moved significantly faster when tadpoles were still present compared to the consecutive
351 homing (GLMM estimates \pm standard errors: with tadpoles 0.132 ± 0.015 ; without tadpoles
352 0.092 ± 0.017 ; $p=0.02$; see also Table 1 summarizing the raw data). Results from our model
353 investigating effects of weather on the movement speed of frogs can be found in the
354 supplemental information: Table S1, S2).

355

356 Pool visits

357 We recorded 49 pool visits during 28 TTs (20 tagged individuals) including all artificial and
358 natural, available and removed/dry pools. Frogs carried on average 8.5 tadpoles (sd = 4.9, n = 27;
359 1 excluded) and were never observed to visit further pools after finishing deposition. In 25 of the
360 28 TTs, successful deposition of tadpoles was recorded. The remaining 3 individuals lost the
361 tadpoles overnight (n = 1), were predated by a spider (n = 1) and disappeared while tracking
362 (n=1). From the 49 pool visits recorded, deposition happened in 29 cases (artificial pools = 26

363 times, natural deposition sites = 3 times) and no deposition took place in 20 cases (removed
364 artificial pool = 11 times, dry natural pool = 6 times, available artificial pool = 3 times). The
365 distance from the first observed pool visited by each frog ($n = 28$) to the territory center was on
366 average 41.07 m (range = 2.1–98.33 m). During the tracked TTs, male frogs visited on average
367 2.4 depositions sites per transport event ($n = 15$, range = 1–4, including removed and desiccated
368 pools). However, we cannot exclude that frogs had visited other deposition sites before being
369 encountered.

370

371 Movement precision

372 Frog movement was strongly directed towards potential deposition sites and the home territory
373 for TTs and HTs, respectively (see Fig. 2, 3 and Fig. S2). For the directionality analysis, we only
374 used tracks with more than three locations. The tadpole carriers ($n = 14$, 10 individuals; 1
375 excluded) moved directly to and between potential deposition sites with an average straightness
376 coefficient of 0.76 ($sd = 0.21$), an average angular deviation of 24.52° ($sd = 36.58^\circ$; Rayleigh test
377 $p < 0.001$) and an average linear deviation of 2.9 m ($sd = 4.02$) from the straight-line path. On
378 their way back to the home territory, frogs ($n = 22$, 16 individuals) reached an average
379 straightness coefficient of 0.87 ($sd = 0.12$) and moved with an average angular deviation of
380 32.28° ($sd = 42.58^\circ$; Rayleigh $p < 0.001$) from the ideal path and an average linear deviation of
381 2.04 m ($sd = 2.03$).

382 Movement precision during TTs: None of the models with SC, average angular deviation or
383 average distance to the straight-line path as response variable and heading towards an available
384 or unavailable pool as explanatory variable improved the AICc compared to their corresponding

385 null model. Thus, we could not find any difference in the frog's movement behavior when
386 encountering a removed or available pool (Table S5).

387 Movement precision during homing: The two models with the response variables SC or average
388 distance to straight line and heading towards an available or unavailable pool as explanatory
389 variable did not improve the AICc compared to their corresponding null model. For the model
390 with average angular deviation as response variable, the AICc of the full model was lower
391 compared to the corresponding null model ($\Delta\text{AICc} = 2.59$), but there was no difference between
392 the levels of the explanatory variable (GLMM estimates \pm standard errors: heading towards an
393 available pool 28.733 ± 4.860 ; heading towards non-available pool 29.580 ± 6.625 ; $p = 0.9$).
394 Overall, this indicates that there is no difference during homing between frogs which did and did
395 not encounter an unavailable deposition site during tadpole transport (Table S6).

396

397 **Discussion**

398 Movement patterns

399 In our study, we quantified movements of tadpole-transporting frogs, reflecting different costs
400 and benefits during exploitation of dispersed reproductive resources. Surprisingly, we did not
401 observe any exploratory behavior of *A. femoralis* during tadpole transport or subsequent homing.
402 Males exhibited highly directed movement towards deposition sites and, in contrast to our
403 predictions, also on the way back to their home territory. Long distance movements have many
404 potential costs for breeding males such as energetic expenditures, exposure to predation, lost
405 mating opportunities, and the risk of losing the territory altogether (Bell, 2012). During the TT
406 these costs may even be higher, as offspring survival has also to be taken into account (Downie
407 et al., 2005). To minimize travel distance and time, straight movement towards previously

408 learned deposition sites and the home territory saves time and likely reduces these risks. Thus,
409 we suggest that the risks and costs of exploratory behavior during tadpole transport and homing
410 outweigh potential benefits for breeding males.

411 During the breeding season male *A. femoralis* are mostly found in their territories, exhibiting
412 prolonged calling activity to attract females and to repel competing males, especially in the
413 afternoon (Kaefer et al., 2012). Male mating success in *A. femoralis* was found to be determined
414 by the possession of a territory (Ursprung et al., 2011) and probably calling activity and territory
415 size (Roithmair, 1992). Exploration during the tadpole transport could lead to lost mating
416 opportunities and even territory loss, thereby decreasing mating success and hence the individual
417 fitness of males. In *A. femoralis* exploration of the habitat apparently occurs during different
418 periods, likely when there are less costs imposed on males, compared to the active breeding
419 phases. In male *Dendrobates auratus* exploratory behavior was not only reported after tadpole
420 transport, but also during short detours from their territory (Summers, 1989). In *A. femoralis*,
421 territorial displacements as well as spontaneous territorial shifts have been observed both within
422 and between reproductive seasons (Ringler, Ursprung & Hödl, 2009), and are particularly
423 common at the onset of reproduction (personal observation MR, AP). Such shifts may provide
424 less costly opportunities to explore the surrounding area and update the information on pool
425 availability. In addition, very little is known about *A. femoralis* movements outside of the
426 breeding season, and in particular about their movement patterns during the juvenile phase, when
427 learning of potential deposition sites might be less costly than during breeding. Indeed, we have
428 regularly observed juveniles as well as adult frogs in the immediate vicinity of water-filled
429 artificial pools during dry periods, when calling and reproductive activity is low (personal
430 observation MR, AP). However, complete pool desiccation during the dry season and the natural

431 dynamics of small natural pools suggest that exploration during juvenile dispersal and the non-
432 reproductive season alone would not provide sufficient information for efficient tadpole
433 transport.

434

435 The movement of *A. femoralis* during tadpole transport and homing was characterized by stop-
436 and-go phases of varying duration and speed. Intermittent movement patterns can be found in
437 many organisms ranging from protozoans to mammals, and in a variety of behavioral contexts
438 such as searching or habitat assessment. Frequent stop phases can lead to perceptual benefits as
439 animals have time to scan the area, and conspicuousness towards predators might be reduced
440 (Kramer & McLaughlin, 2001). Hence, the stop-and-go locomotion pattern of male frogs during
441 tadpole shuttling and homing could be a further adaption for orientation and resting, while
442 reducing risks related to continuous movement.

443 We found that movement speed was significantly higher when tadpoles were carried compared
444 to speed after deposition had been finished. As it has been shown in another poison frog species
445 (Smith et al., 2006) the presence of tadpoles does not seem to inhibit the locomotory
446 performance of transporting frogs. We assume that overall costs during tadpole transport are
447 higher than during homing, as the survival of the transported offspring also has to be accounted
448 for. As a result, frogs appear to adjust their movements and quickly deposit their offspring to
449 prevent for instance desiccation of tadpoles (Downie et al., 2005). However, why frogs are
450 slower during homing, remains unclear. Since frogs do not appear to explore during homing,
451 faster homing should reduce the risk of losing mating opportunities (Roithmair, 1992; Ringler et
452 al., 2013), or the entire territory which might even include further clutches. Potential exhaustion
453 after tadpole deposition, time needed for homewards orientation or high risk of predation during

454 fast movement might explain slower movement during homing, but future studies need to
455 examine these factors in more detail.

456

457 Pool visits

458 During the entire study, we never observed male frogs that encountered a removed artificial or
459 dry natural pool to exhibit any exploratory behavior after the deposition of tadpoles. Two
460 individuals that encountered an unavailable deposition site, were observed during a second
461 tadpole transport event when they visited the very same unavailable pool. In contrast to our
462 predictions, the actual availability of potential deposition sites had little influence on the
463 movement patterns of male frogs, and no apparent updating of information about resource
464 availability during tadpole transport occurred. In our study, all frogs except one (which lost
465 tadpoles overnight) managed to find an available pool for deposition even if they had previously
466 encountered a removed or dry pool. Further, we recorded one male visiting a natural pool site,
467 which never held water during the entire study period and was only known as a potential
468 deposition site from previous years. These findings suggest that male frogs predominantly rely
469 on their spatial memory to find deposition sites and do not invest time and energy in exploring
470 further pools during tadpole transport. Despite the rapidly changing weather conditions in the
471 tropics, resource availability seems to be sufficiently stable for frogs to rely on memory based
472 orientation strategies. Unavailable pools might turn into available breeding resources after one
473 heavy rainfall, whereas some pool locations remain the same during the entire season and over
474 years. Thus, previously visited pools can be remembered as having been available in the past and
475 to be at least physically suitable to hold water. The best strategy might be to remember previous
476 sites and visit them repeatedly, even at the risk that they might have vanished since the last visit.

477 Further, our results did not reveal any influence of pool-associated cues, such as odor, on frog
478 orientation accuracy. We did not find any difference when comparing the precision and speed of
479 frogs that moved towards an available or unavailable deposition site. Olfaction, however, might
480 still play a role in the initial discovery of new deposition sites and spatial orientation in this
481 species (Pašukonis et al., 2016).

482 Recent tracking and genetic studies have revealed that *A. femoralis* remember the location of up
483 to six different pool sites (Pašukonis et al., 2016) and that frogs actively partition their offspring
484 across several water bodies as a possible reproductive bet-hedging strategy (Erich et al., 2015).
485 Our results corroborate these findings as tracked individuals carried on average nine tadpoles
486 (whereas clutches contain up to 20 eggs) and visited and used two to three deposition sites per
487 tadpole transport event. However, we cannot entirely rule out that some of our observed
488 movements between multiple pool sites might be a byproduct of disturbances from tracking and
489 handling. About half of the tracked males did not move to the pool closest to their territory for
490 deposition. If tadpole distribution over several distant sites improves offspring survival, then
491 knowing more pool locations should have direct fitness consequences. However, we speculate
492 that there is a trade-off between minimizing the costs of tadpole transport and maximizing the
493 potential benefits gained through offspring partitioning over multiple learned sites.

494

495 **Conclusions**

496 While it remains unknown when and how the poison frog *A. femoralis* collects information about
497 the surrounding area, we provide, for the first time, detailed information about the movement
498 patterns during tadpole transport. Despite extensive capture-recapture studies (Ringler, Ursprung
499 & Hödl, 2009), and some tracking of *A. femoralis* after translocations (Pašukonis et al., 2014a,b)

500 and tadpole transport (Pašukonis et al., 2016), still very little is known about the natural
501 movement patterns of poison frogs during tadpole transport and the potential influencing factors.
502 We observed highly directional movement, indicating that quick tadpole transport and homing
503 has a higher net-benefit compared to potential advantages gained through additional exploratory
504 detours. Future research should investigate in more detail the costs of tadpole transport and
505 territorial behavior to understand the trade-offs shaping movement strategies in complex
506 dynamic environments, as well as the mechanisms that allow poison frogs to orientate with such
507 high precision in the rainforest. Long-term tracking during and at the onset of the breeding
508 season will be necessary to further investigate when and how poison frogs collect knowledge
509 about the environment. In addition to field work, agent-based modeling could be a useful tool to
510 test different strategies related to tadpole transport, exploration and memory.

511

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516

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Table 1 (on next page)

The average speed of frog movement

The sections TT and HT are summarized by minimum, maximum 1st and 3rd quartile, median and mean.

1

	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
Speed during TT	3.01	8.77	12.44	10.16	14.87	17.15
(m/h)						
Speed during HT	2.64	4.12	6.14	7.22	9.62	21.67
(m/h)						

2

3

Figure 1

Map of the study area

Experimental setup and the distribution of male territories in the study area. Red asterisks represent tracked frog territories (n=16) and white asterisks represent the territories of other identified males in the area (n=49). Squares represent the cross-array of thirteen artificial tadpole deposition sites, blue squares representing available pools and gray crossed squares the removed deposition sites. Blue circles represent four potential natural pools, which were visited by tadpole carriers during tracking. Contour lines (1 m) and the Arataye River are drawn in light gray.

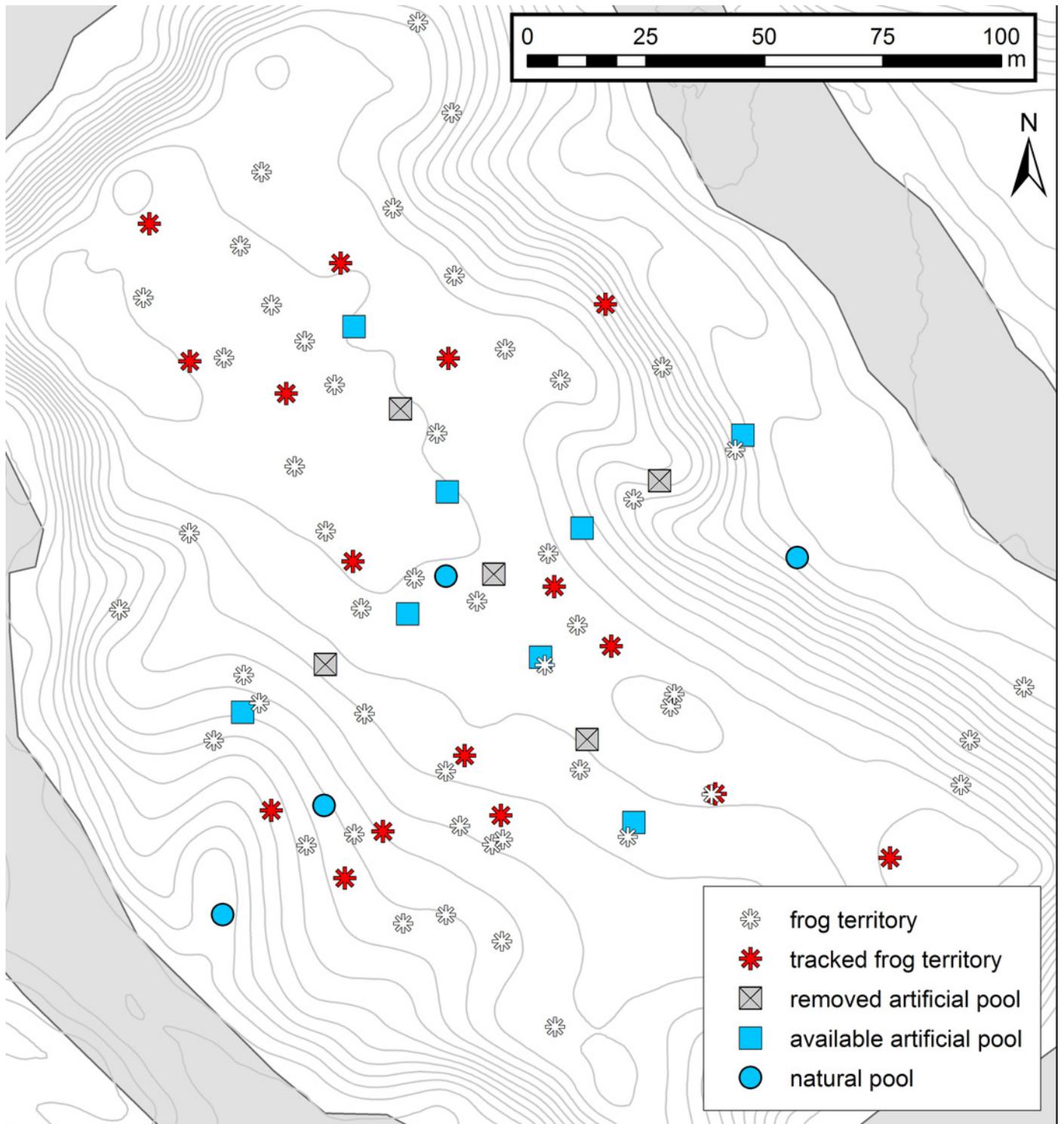


Figure 2

Tadpole transport trajectories

Trajectory map showing movement patterns of tadpole transporting males to and between the deposition sites. Different colors represent different tracking events (n=15, 10 individuals), full lines represent the frog paths obtained by interpolating the consecutive frog locations and dashed lines the missing path from the territory to the first encounter point. For all other symbols see Fig. 1.

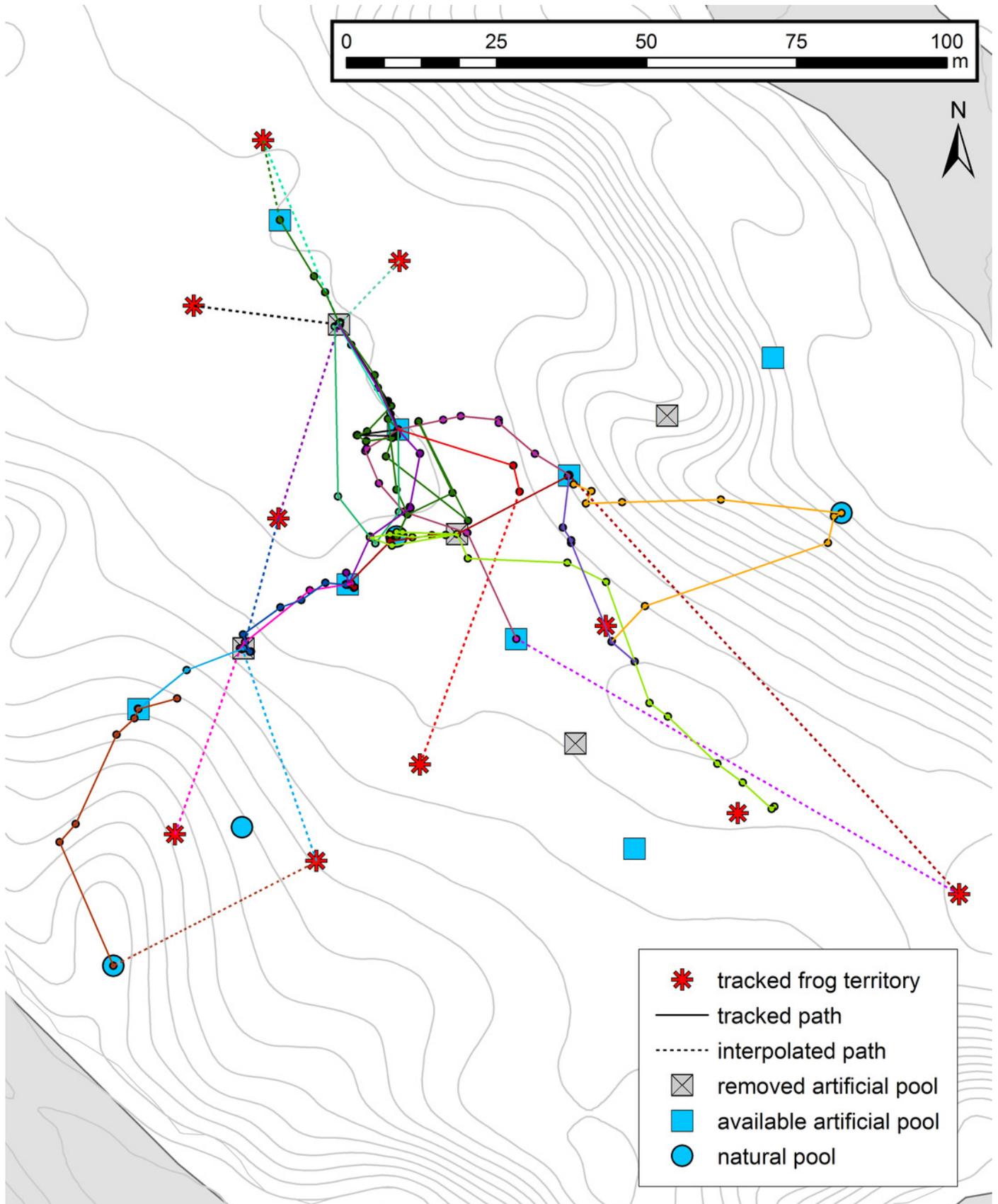


Figure 3

Homing trajectories

Part of a polar plot showing the HTs of male frogs (each colored line represents one HT, $n=22$, 16 individuals). All trajectories were normalized to a single starting point (center of the plot) and show the first 100 m of homing.

