

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 their 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 movement phases. 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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25 **Abstract**

26

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

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

47 *femorialis*. Our study provides for the first time a detailed description of poison frog movement
48 patterns during tadpole transport and corroborates recent findings on the significance of spatial
49 memory in poison frogs. When these frogs explore and discover new reproductive resources
50 remains unknown.

51

52 **Introduction**

53 In a dynamic environment resource availability changes in time and space which has major
54 influences on animal movement decisions (Milner-Gulland, Fryxell & Sinclair, 2011; Bell,
55 2012). Animals that rely on unpredictable, ephemeral, and patchy resources have to explore their
56 environment regularly (Roshier, Doerr & Doerr, 2008). Updating information on profitable
57 resources can be achieved by exploring unknown areas to collect new information, by frequently
58 visiting already known patches to affirm the availability of resources, or by prospecting for new
59 resources within familiar areas (Real, 1981; Eliassen et al., 2009; Díaz et al., 2013). However,
60 exploration comes at a cost of the time spent searching, which conflicts with other fitness-related
61 activities such as territory defense (cf. Ydenberg & Krebs, 1987) and advertising for mates
62 (Thomas et al., 2003). Exploration also increases the exposure to sit-and-wait predators and thus
63 overall predation risk (Stamps, 1995). Thus, animals depending on fluctuating resources need to
64 find a balance between relying on known resources and prospecting for new ones (Milner-
65 Gulland, Fryxell & Sinclair, 2011).

66 Most amphibians depend on aquatic sites for breeding, making this taxon particularly suitable for
67 investigating how animals deal with varying availability, stability and distribution of resources.
68 Amphibians exhibit a great diversity of reproductive strategies ranging from explosive breeders
69 that gather at large ponds for synchronized spawning, to prolonged breeders with terrestrial

70 clutches that use small widespread pools for tadpole development (Duellman & Trueb, 1994;
71 Crump, 2015). Tropical amphibians, in particular, are renowned for the variety of aquatic sites
72 that they use for reproduction (Wells, 2007). Despite the overall large amount of rainfall,
73 seasonal variability can have a strong impact on the availability of breeding resources and thus
74 on the reproductive success of tropical amphibians (Aichinger, 1987; Bertoluci & Rodrigues,
75 2002; Gottsberger & Gruber, 2004). During heavy rainfall, potential breeding sites such as small
76 pools in the ground can appear within hours. However, desiccation also happens rapidly due to
77 the high environmental temperatures. To date, it remains mostly unknown how tropical
78 amphibians deal with the uncertainty of breeding sites, and which mechanisms they use to find
79 these scattered resources.

80 The Neotropical poison frogs (Dendrobatidae) exhibit a variety of complex spatial behaviors
81 such as territoriality, tadpole transport, and offspring provisioning (Weygoldt, 1987; Pröhl, 2005;
82 Lötters, 2007). The complex parental behavior in this group of frogs has attracted a considerable
83 amount of research (e.g. (Brown, Morales & Summers, 2008; Dugas et al., 2015; Ringler et al.,
84 2015; Schulte & Summers, 2017); for reviews see (Wells, 2007; Summers & Tumulty, 2013;
85 Roland & O'Connell, 2015)). However, the associated movement patterns and the factors
86 shaping them have rarely been quantified and remain poorly understood (but see (Summers,
87 1990; Brown, Morales & Summers, 2009; Ringler et al., 2013)). Most poison frogs show site
88 fidelity to their territory and shuttle their larvae from terrestrial clutches to widespread,
89 ephemeral deposition sites, where the larvae complete their development (e.g. *Ameerega*
90 *trivittata* and *A. femoralis*, (Roithmair, 1992); *Ranitomeya imitator* and *R. variabilis* (Brown,
91 Morales & Summers, 2009); *R. reticulata* (Werner et al., 2010); *Colostethus panamansis* (Wells,
92 1980); *Dendrobates auratus* (Summers, 1990); *D.leucomelas* and *Oophaga histrionica*

93 (Summers, 1992); for reviews see (Weygoldt, 1987; Pröhl, 2005; Wells, 2007)). When
94 transporting their offspring, frogs need to know when and where to go for suitable water bodies
95 that are persistent enough to allow larval development, but ephemeral enough to minimize
96 predator abundance (cf. Murphy, 2003; Lehtinen, 2004). Recent studies have shown that poison
97 frogs can use flexible learning strategies in spatial tasks in captivity (*Dendrobates auratus*, (Liu
98 et al., 2016)) and rely on prior experience to successfully return home after translocation
99 (*Allobates femoralis*, (Pašukonis et al., 2013, 2014a)) and to find tadpole deposition sites in the
100 field (Pašukonis et al., 2016). Further, two poison frog species have been shown to use spatial
101 rather than direct cues for offspring recognition (Stynoski, 2009; Ringler et al., 2016b). Together
102 these results suggest that poison frogs rely on spatial memory to successfully navigate in their
103 environment, which raises the question of when and how these frogs gain information about the
104 area and in particular how they update information on the availability of their reproductive
105 resources. To date, exploratory behavior has only been reported in two poison frog species in the
106 form of prospecting trips after tadpole deposition, between tadpole transport events (*D.*
107 *auratus*,(Summers, 1989)) or prior to tadpole deposition (female *Oophaga pumilio*, (Brust,
108 1990)). However, the detailed movements during transport and exploration have not been
109 quantified for any poison frog species. In this study, we attempted to fill this knowledge gap by
110 tracking the well-studied poison frog *Allobates femoralis* during tadpole transport.

111 *Allobates femoralis* is a small territorial poison frog with predominantly male tadpole transport
112 (Ringler et al., 2013). Males spread their tadpoles across multiple, scattered aquatic sites; it has
113 been suggested that this approach increases offspring survival (Erich et al., 2015). Their
114 dependency on unpredictable resources and experience-based navigation make *A. femoralis* an
115 ideal study species to address questions concerning the mechanisms and timing of environmental

116 exploration and learning. The demonstrated ability of *A. femoralis* to navigate to locations with
117 high spatial precision (Pašukonis et al., 2014a,b, 2016) makes it easier to interpret their
118 movement patterns, as it suggests that non-directed movement in the local area is more likely to
119 be exploratory behavior than an inability to orient in space. Since tadpole transport constitutes
120 the most prominent long-distance movement in *A. femoralis* (Ringler, Ursprung & Hödl, 2009;
121 Ringler et al., 2013) it has been postulated that the frogs update their knowledge about the area
122 by exploring during tadpole transport and subsequent homing (Pašukonis et al., 2013, 2014b).
123 During the tadpole transport male frogs usually leave their territory, which provides them with a
124 chance to gain information on resource location and quality. However, such exploration during
125 tadpole transport would result in a trade-off between the potential benefits gained and the costs
126 related to searching behavior. During the breeding season, male *A. femoralis* are mostly found in
127 their territories, calling to attract females and to repel competing males (Kaefer et al., 2012).
128 Leaving the territory to explore would increase the risk of losing mating opportunities, losing the
129 entire territory, and can increase energetic expenditure as well as the risk of predation (e.g.,
130 Wolf, Hainsworth & Gill, 1975; Townsend, 1986; Roithmair, 1992). Tadpole transport consists
131 of two phases: first, shuttling the tadpoles until deposition, then homing back to the territory.
132 Exploratory behavior on the way to known deposition sites would also incur potential costs for
133 the offspring being transported, such as increased risk of desiccation (Downie et al., 2005),
134 whereas during homing it would only incur costs for the male. Thus, the net benefit of
135 prospecting for new deposition sites during homing should be higher, which might be reflected
136 in frog movement patterns.

137 In this study we quantified the movement patterns associated with tadpole transport and factors
138 that potentially influence them: attraction to cues originating from the pools, pool desiccation,

139 and the weather. We used telemetry to follow transporting male *A. femoralis* towards artificial
140 deposition sites and back to their territory. To examine whether the frogs performed any
141 exploratory behavior we attempted to induce exploration by removing artificial pools to simulate
142 desiccation. We predicted that tadpole carriers would show fast, directional movement to known
143 pools, as we expected them to aim at reducing potential costs for the transported offspring and to
144 tend to perform exploratory detours on the way back to their territories. Further, we expected
145 frogs encountering a location where a pool had been removed before deposition to be more likely
146 to perform exploratory detours and to continue visiting other deposition sites to update their
147 information on pool availability.

148

149 **Materials & Methods**

150 Study species and area

151 *Allobates femoralis* is a small diurnal frog (snout-urostyle length approximately 25 mm)
152 common throughout Amazonia and the Guiana Shield (Amézquita et al., 2009). During the rainy
153 season males occupy territories (average defended area: 151.13 m² (Ringler et al., 2011)) which
154 they advertise by calling and defend for up to several months (Roithmair, 1992; Ringler,
155 Ursprung & Hödl, 2009). Mating and oviposition of approximately 20 eggs take place in the leaf
156 litter inside the male's territory (Roithmair, 1992; Ringler et al., 2012). After 15–20 days of
157 development, the male revisits the clutch, allows the tadpoles to wriggle onto his back, and
158 transports them to widely distributed deposition sites. On average, males are found with 8
159 tadpoles when transporting (range 1–25, cf., Ringler et al., 2013), and they can deposit them at
160 several pools (Erich et al., 2015). Females will transport the offspring only when males disappear
161 (Ringler et al., 2015). The frogs use a variety of small to medium-sized terrestrial water bodies

162 such as rain-flooded depressions, holes in fallen trees, or palm bracts for tadpole deposition, and
163 recent tracking revealed that *A. femoralis* remember the location of at least six different pool
164 sites (Pašukonis et al., 2016). Aquatic deposition sites constitute a limiting resource for *A.*
165 *femoralis*, and frogs readily use artificial pools when provided in their natural habitat (Ringler,
166 Hödl & Ringler, 2015).

167 We carried out the study from 18 January–12 March 2015 in a lowland rainforest on a 5 hectare
168 river island near the “Camp Pararé” field site at the CNRS “Nouragues Ecological Research
169 Station” in the Nature Reserve “Les Nouragues”, French Guiana (3°59′N, 52°35′W) (Bongers et
170 al., 2013; Ringler et al., 2016). All necessary permits were provided by the Centre National de la
171 Recherche Scientifique (CNRS) and by the Direction Régionale de l’Environnement, de
172 l’Aménagement et du Logement (DEAL: ARRETE n°2011-44/DEAL/SMNBSP/BSP). The
173 island population was established by introducing 1800 genotyped *A. femoralis* tadpoles from a
174 nearby population in 2012 (Ringler, Mangione & Ringler, 2014) that were released in artificial
175 pools (volume ~12 l, inter-pool distance ~10 m). In 2013, the pools were rearranged in a cross-
176 shaped array of 13 pools (inter-pool distance ~20 m). At the beginning of our study in 2015 we
177 removed every second pool to experimentally simulate dried-up water bodies, leaving 8 pools
178 available (Fig.1). Occasionally, tadpole carriers also used natural deposition sites such as small
179 flooded depressions and burrows on the forest floor. In total, we recorded four such natural sites
180 which temporarily filled with water, depending on the weather conditions, and which were
181 visited by tadpole-transporting frogs during our study (Fig.1).

182

183 Territory sampling

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

193

194 Tadpole carrier tracking

195 Because *A. femoralis* clutches are difficult to find and the timing when the male picks up the
196 tadpoles is variable (personal observation S. Weinlein), we focused our search effort on finding
197 frogs already transporting tadpoles, mostly by searching around known deposition sites.

198 Sampling was done every day between 0700 and 1300 h as tadpole transport mainly occurs in the
199 morning (Aichinger, 1987; Ringler et al., 2013). We caught the tadpole carriers in transparent
200 plastic bags, photographed them for identification, and recorded their exact position on the GIS
201 map. We counted the number of transported tadpoles, and when some tadpoles fell off during
202 catching and handling, we placed them on the male's back again.

203 Before the release, we equipped transporting males with a transponder attached to a waistband
204 (Fig. S1). The entire procedure took a few minutes and did not disrupt tadpole transport or
205 deposition behavior regardless of whether the tadpoles were manipulated or not. We followed
206 tagged tadpole carriers using the harmonic direction-finding (HDF) telemetry technique. This

207 system consists of a passive reflector/transponder, which is attached to the animal and an active
208 directional transceiver, which emits and then receives the reflected radio signal. It allows smaller
209 animals to be tracked than would be possible by conventional active radio tracking (Mascanzoni
210 & Wallin, 1986; Rowley & Alford, 2007), and it has been successfully used in *A. femoralis*
211 (Pašukonis et al., 2014a,b). We fitted the tags using a silicon tube 2 mm in diameter, forming a
212 waistband with an additional strap between the hind legs to prevent the tag from rotating (Fig.
213 S1). Both parts were fixed with a cotton thread, which would break and release the waistband
214 after approximately two to three weeks (personal observation KB, AP) in case an individual was
215 not recaptured. The waistbands carried a small diode beneath a color-coded seal and a T-shaped
216 dipole antenna made of flexible, coated wire. The long end (~12 cm) of the antenna dragged
217 freely behind the moving frog while the short end (~2 cm) was secured inside the waistband. As
218 *A. femoralis* is strictly diurnal, we only tracked frogs during daylight hours (0700–1900 h),
219 relocating each individual and recording their position every 30–60 min. We followed each frog
220 until all tadpoles had been deposited and the male had returned to his territory, where the tag was
221 removed. We assumed that the frogs had returned when they approached locations at which they
222 had previously displayed territorial behavior. During tracking we tried to minimize disturbance
223 by carefully approaching the signal source while searching with the transceiver until the frog was
224 visually spotted or the origin of the signal could be narrowed down to less than 1 m. We
225 approached individual frogs from different directions so as to not influence or bias their
226 movement in any direction. Occasional disturbances during tracking only influenced our
227 measurements of the directionality of long distance movements minimally, because *A. femoralis*
228 responds to disturbance by immediately hiding in the leaf litter rather than fleeing over longer
229 distances (personal observation KB, MR, AP). We caught tagged individuals when they had not

230 moved for more than a day to check for possible issues such as skin injuries – in a single case we
231 immediately removed the tag. In one case without movement for more than two days but without
232 apparent injuries we also removed the tag to minimize any potential long-term effects on
233 behavior.

234

235 Tracking data

236 We handled and visualized spatial data in the GIS software ArcGIS10 (ESRI) after projecting
237 (UTM-zone 22N, WGS1984), and all analyses were performed in the statistical software R
238 version 3.2.0 (Team, 2014). We split the full trajectories of tracked frogs into tadpole transport
239 (TT) from the first encounter point to the last deposition site, and homing trajectories (HT), from
240 the last deposition site back to the home territory. Movement distance, duration, and speed were
241 calculated for each TT and HT. For individuals that took more than one day to complete
242 deposition and/or homing, we excluded the nights (-12 h per night) to estimate the average time
243 they were moving during tadpole transport. In most cases, the observed TT did not cover the full
244 TT as the frogs were encountered on their way to the pools or in their close vicinity. We
245 excluded individuals encountered immediately before tadpole deposition (frogs already present
246 at a pool or individuals with fewer than 2 tracking locations recorded before reaching the pool)
247 from the analysis of TT trajectories. We interpolated the total distances of TTs by approximating
248 the missing part from the territory center until the first encounter location by a straight-line to
249 obtain minimum-distance estimates (see Fig. 2).

250

251 ***Influence of tadpoles on movement speed:*** We created a generalized linear mixed model
252 (GLMM) to test the effects of tadpole presence (TT vs. HT) on the movement speed of frogs

253 (family = gamma, link = logit). As response variable, we used the average speed per TT and HT,
254 as explanatory variable “tadpoles present” (yes/no), and individual frog ID as random factor to
255 account for repeated trajectories of the same individuals.

256

257 ***Influence of weather on movement speed:*** Since frog activity varies throughout the day and
258 depends on weather conditions (Bellis, 1962; Brooke, Alford & Schwarzkopf, 2000), we
259 investigated potential effects of the weather on the frogs’ movement speed using temperature and
260 rainfall measurements, both obtained from an above-canopy weather station (Nouraflux: rainfall
261 sensor Campbell ARG100, temperature sensor Vaisala HMP155A). In contrast to the previous
262 model, where the focus was on certain trajectory sections (TT and HT), we focused on 3 h
263 intervals here to investigate variations in the frogs’ activity (here: movement speed). The 3 h
264 intervals represent four potentially different daily activity periods in *A. femoralis*, with tadpole
265 transport happening predominately in the morning, low activity around noon, high calling
266 activity during the afternoon, and high calling activity and most female-male interactions (e.g.,
267 courtship) in the evening (personal observation by all authors; see also (Kaefer et al., 2012;
268 Ringler et al., 2013)). We used a GLMM (family = gamma, link = logit), with speed as response
269 variable, and the explanatory variables “tadpoles present” (yes/no), “time of the day” (split in
270 four 3 h intervals: 0700-1000, 1000-1300, 1300-1600, 1600-1900 h), average “temperature” for
271 each corresponding interval, and cumulative “rain” in millimeters during each interval. Since this
272 analysis is not within the main focus of this study, we present the results in the supplemental
273 information (Table S1, S2).

274

275 Pool visits

276 We defined a pool visit as frogs actually entering a potential deposition site (position either on/in
277 a filled pool or on the removed/dried out pool location). For each tadpole carrier, we recorded all
278 potential tadpole deposition sites visited (available/removed artificial pool or available/dried-out
279 natural site), and whether tadpole deposition occurred at the available pools or not. To test
280 whether frogs explored further pools after the complete deposition of their offspring, we
281 recorded for each location whether there were tadpoles still present on their back or not. If frogs
282 moved to further pools without tadpoles on their back, we considered this to be exploratory
283 behavior. In addition, we calculated the average number of deposition sites the frogs visited
284 (available/removed artificial pool or available/dried-out natural site) per tadpole transport. We
285 excluded trajectories with only one final deposition site and no detailed TT.

286

287 Movement precision

288 To investigate whether frogs explored the surrounding area by taking additional detours, we
289 estimated the precision of the frogs' orientation towards the upcoming pools during TTs, and
290 towards the territory during the HTs. To estimate navigation precision, we calculated three
291 different parameters: (1) the straightness coefficient (SC) of the trajectory, (2) the average
292 angular deviation between the ideal orientation angle and consecutive tracking locations, and (3)
293 the average normal distance of tracking locations from the straight-line path. The SC is defined
294 as the ratio between the straight-line distance to the respective goal and the actual path distance.
295 SC ranges from 0 to 1 with 1 indicating a perfectly straight trajectory. The angular deviations
296 were measured as the absolute angular difference between the ideal direction (angle from each
297 tracking location to the respective goal) and the actual direction of the individual frog's
298 movement (angle from each tracking location to the next one). For the distance of the frog's

299 movement from the straight-line path, we calculated the perpendicular deviation of each tracking
300 location from the straight path. While the SC takes into account the entire trajectory at once, the
301 average angular deviations describe the movement decisions from location to location, and the
302 distance from the straight-line path assesses the frog's position in relation to the straight line for
303 every location. We calculated the mean angular deviation and distance from the straight-line path
304 by averaging all values per TTs and HTs in order to have three precision measurements per TTs
305 and HTs.

306 We tested for significant goal-directed orientation using absolute angles calculated with the
307 "as.ltraj" function from the package "adehabitatLT" (Calenge, 2015) per TTs and HTs using
308 Rayleigh tests with the package "circular" (Agostinelli & Lund, 2011).

309

310 ***Influence of pool availability on movement precision:*** In addition, we tested whether the
311 precision during TTs differed (for example resulting from olfactory cues from the water), when
312 tadpole carriers approached an available deposition site (artificial or natural pool) or an
313 unavailable pool site (removed or desiccated). Therefore, we compared the precision of TTs (SC,
314 average angular deviation and average distance from the straight line path per trajectory) of frogs
315 that were heading towards available and non-available pools. We used different GLMMs with
316 the "SC" (family = beta, link = logit), "average angular deviation" (family = gamma, link = logit)
317 and "average distance to the straight-line path" (family = gamma, link = logit) as response
318 variable. For all three models, we used "heading towards an available vs. non-available pool" as
319 explanatory variable and individual frog ID as a random effect.

320 Finally, we investigated potential differences in precision along the tracked HTs between frogs
321 that either did or did not encounter a site with a non-available pool (removed pools and naturally

322 dried-out water bodies) during prior tadpole transport. For the analysis, we used different linear
323 mixed models (LMM), with “average angular deviation” and “average distance from the straight-
324 line path” as response variable and a GLMM (family = beta, link = logit) with “SC” as response
325 variable. For all three models, we used “removed pool encountered during prior tadpole
326 transport” (yes/no) as explanatory variable and the individual frog ID as random factor to
327 account for repeated trajectories of the same individuals.

328

329 Model selection

330 All the full models but one contained only a single explanatory variable, which was a binary
331 factor. We compared these models with the corresponding null (intercept) model based on the
332 second-order form of Akaike’s information criterion (AICc; (Hurvich & Tsai, 1989)). No
333 difference between the full model and the null model (i.e. $\Delta AICc \leq 2$) indicates that the variation
334 of the response variable is not explained better by the full model than by the null model
335 (Burnham & Anderson, 2002). If this is the case the null hypothesis is supported and we
336 therefore do not present the model parameters in the results. For the model with several
337 explanatory variables we created all possible candidate models (all-subset modeling) following
338 the information-theoretic approach (Burnham & Anderson, 2002). We ranked them according to
339 their AICc values and selected those within $\Delta AICc \leq 2$ with respect to the top-ranked model. We
340 estimated parameters for each explanatory variable included in the $\Delta AICc \leq 2$ subset by model
341 averaging (following Burnham & Anderson, 2002).

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

345

346 **Results**347 Frog sampling and movement analysis

348 During the study period, we captured 67 individual males a total of 658 times. 408 captures were
349 associated with male territorial behavior and were used to calculate territory centers (Fig.1). We
350 observed 50 tadpole transports by 30 males and tagged 20 individuals, which allowed us to track
351 28 tadpole transports. From all tagged frogs, we used the TTs and/or HTs of 16 individuals for
352 movement analysis: n = 15 TTs from 10 individuals (including five individuals with 2 TTs each);
353 n = 22 HTs from 16 individuals, (including one individual with 3 HTs and four individuals with
354 2 HTs each). Other trajectories were excluded because some individuals had either not moved
355 further than 5 m for two days (n = 1), had an injury (n = 1), were predated on by a spider (n = 1),
356 or the entire tadpole transport took place inside their territory (n = 1). All averaged values (i.e.,
357 distance, time and speed) were estimated by first averaging per trajectory section (TT and HT),
358 followed by calculating the overall average from all TTs and HTs.

359 Summing up the entire trajectory (interpolated start + TT + HT; n = 14, 10 individuals) frogs
360 moved an average of 141.73 m (sd = 68.87 m, range = 59.94–276.01 m) and were tracked for an
361 average of 17.62 h (sd = 14.01, range = 6.42–58.4 h, nights excluded). Tracked TT (n = 15, 10
362 individuals, see Fig. 2) covered a distance of 56.34 m (sd = 38.09 m, range = 4.93–141.37 m) on
363 average. The interpolated path was 39.21 m (sd = 24.72 m, range = 0–95.16 m, for n = 12, 7
364 individuals) on average, adding up to an average distance of 87.71 m (sd = 40.29 m, range =
365 35.32–166.43 m) for the whole TT. The elapsed time until all tadpoles were deposited was 5.55 h
366 (sd = 2.7 h, range = 2.08–13.25 h, nights were excluded for n = 1) on average. The speed during
367 tracked TTs was on average 10.16 m/h, reaching a maximum of 17.91 m/h (averaged over the

368 entire TTs, distance = 55.16 m, time = 3.08 h; for further details see Table S3). During HTs,
369 male frogs moved an average distance of 54.57 m (sd = 29.63 m, range = 15.98–123.46 m, n =
370 22, 16 individuals, see Fig. S2) and the average time elapsed until their return to the territory was
371 10.78 h (sd = 10.38 h, range = 1–49.9 h, nights were excluded for n = 10). Speed during homing
372 was 7.22 m/h on average with a maximum of 22.16 m/h (averaged over the entire HTs, distance
373 = 22.16 m, time = 1 h; for further details see: Table S4). The movements during the TTs and the
374 HTs were characterized by stop-and-go phases varying in speed (range of speed from one
375 tracking location to the next one = 0–70.12 m/h, for further details see Figure S3 and S4).
376 Frogs moved significantly faster when tadpoles were still present compared to the subsequent
377 homing (GLMM estimates \pm standard errors: with tadpoles 0.132 ± 0.015 ; without tadpoles
378 0.092 ± 0.017 ; $p=0.02$; see also Figure 3). Results from our model investigating effects of
379 weather on the movement speed of frogs can be found in the supplemental information: Table
380 S1, S2).

381

382 Pool visits

383 We recorded 49 pool visits during 28 TTs (20 tagged individuals) including all artificial and
384 natural, available and removed/dry pools. Frogs carried on average 8.5 tadpoles (sd = 4.9, n = 27;
385 1 excluded) and were never observed to visit further pools after depositing all their tadpoles. In
386 25 of the 28 TTs, successful deposition of tadpoles was recorded. The remaining 3 individuals
387 either lost the tadpoles overnight (n = 1), were predated on by a spider (n = 1) or disappeared
388 during tracking (n=1). From the 49 pool visits recorded, deposition occurred in 29 cases
389 (artificial pools = 26 times, natural deposition sites = 3 times) and no deposition took place in 20
390 cases (removed artificial pool = 11 times, dry natural pool = 6 times, available artificial pool = 3

391 times). On average, the first observed pool visited by each frog ($n = 28$) was 41.07 m (range =
392 2.1–98.33 m) away from the territory center. During the tracked TTs, male frogs visited an
393 average of 2.4 deposition sites per transport event ($n = 15$, range = 1–4, including removed and
394 desiccated pools). However, we cannot exclude that frogs visited other deposition sites before we
395 encountered them.

396

397 Movement precision

398 Frog movement was strongly directed towards potential deposition sites and the home territory
399 for TTs and HTs, respectively (see Fig. 2, 4 and Fig. S2). We only used tracks with more than
400 three locations for the analysis of directionality. The tadpole carriers ($n = 14$, 10 individuals; 1
401 excluded) moved directly to and between potential deposition sites with an average straightness
402 coefficient of 0.83 ($sd = 0.13$), an average angular deviation of 24.52° ($sd = 36.58^\circ$; Rayleigh test
403 $p < 0.001$) and an average linear deviation of 2.9 m ($sd = 4.02$) from the straight-line path. On
404 their way back to the home territory, frogs ($n = 22$, 16 individuals) reached an average
405 straightness coefficient of 0.87 ($sd = 0.12$) and moved with an average angular deviation of
406 32.28° ($sd = 42.58^\circ$; Rayleigh $p < 0.001$) from the ideal path and an average linear deviation of
407 2.04 m ($sd = 2.03$).

408 Movement precision during TTs: None of the models with SC, average angular deviation or
409 average distance to the straight-line path as response variable and heading towards an available
410 or unavailable pool as explanatory variable improved the AICc compared to their corresponding
411 null model. Thus, we could not find any difference in the frog's movement behavior when
412 encountering a removed or available pool (Table S5).

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

422

423 **Discussion**

424 Movement patterns

425 In our study, we quantified movements of tadpole-transporting frogs, but we did not observe any
426 exploratory behavior of *A. femoralis* during tadpole transport or subsequent homing. Males
427 exhibited highly directed movement towards deposition sites and, in contrast to our predictions,
428 also on their way back to their home territory. Frogs moved faster when transporting the tadpoles
429 than when homing and we found no effect of pool presence (available or unavailable deposition
430 site) on the precision or speed of movement.

431

432 For breeding males, long distance movements can have many potential costs such as energy
433 expenditure, exposure to predation, lost mating opportunities, and the risk of losing the territory
434 altogether (Bell, 2012). Straight movement towards previously learned deposition sites and back
435 to the home territory minimizes both distance and time, thereby reducing such costs. During the

436 TT these costs may even be higher, as offspring survival also has to be taken into account
437 (Downie et al., 2005), which might explain the increased speed during tadpole shuttling. During
438 the breeding season, particularly in the afternoons, male *A. femoralis* are mostly found in their
439 territories, calling to attract females and repel competing males (Kaefer et al., 2012). Male
440 mating success in *A. femoralis* is determined by the possession of a territory (Ursprung et al.,
441 2011) and probably also by calling activity and territory size (Roithmair, 1992). Exploration
442 during the tadpole transport could decrease mating success and hence the individual fitness of
443 males. We suggest that the costs of exploratory behavior during tadpole transport outweigh
444 potential benefits for breeding males, and thus exploration is more likely to occur when males
445 are not currently defending a territory.

446

447 During the breeding season, new artificial pools are used for tadpole deposition within days or
448 weeks, indicating that at least some exploration occurs during the reproductive season ((Ringler,
449 Hödl & Ringler, 2015); personal observation MR and AP). Territorial displacements, as well as
450 spontaneous territorial shifts, have been observed both within and between reproductive seasons
451 (Ringler, Ursprung & Hödl, 2009), and are particularly common at the onset of reproduction
452 (personal observation MR, AP). Such shifts may provide opportunities to explore the
453 surrounding area and update the information on pool availability that are less costly. In addition,
454 very little is known about *A. femoralis* movements outside the breeding season. We have
455 regularly observed juveniles as well as adult frogs in the immediate vicinity of water-filled
456 artificial pools during dry periods, when calling and reproductive activity is low (personal
457 observation MR, AP). Sensitive learning phases during the juvenile stage are common in
458 vertebrates (Immelmann, 1975), but since adult frogs can establish new territories (Ringler,

459 Ursprung & Hödl, 2009) and discover new pools during the breeding season (Ringler, Hödl &
460 Ringler, 2015), the spatial learning mechanism seems to be flexible and open-ended. In addition,
461 both complete pool desiccation during the dry season and disappearance of some pools over time
462 suggest that exploration during juvenile dispersal and the non-reproductive season alone are
463 unlikely to provide sufficient information to the frogs for efficient tadpole transport. Studying
464 juvenile dispersal and the adult movement patterns outside the breeding season, however, will be
465 necessary to fully understand when and how the frogs acquire new spatial information.
466 Furthermore, investigating the learning mechanisms underlying the spatio-cognitive capacity
467 could provide insights into its potential constraints and how animal movement is shaped (Fagan
468 et al., 2013).

469

470 We found that movement speed was significantly higher when tadpoles were still being carried
471 compared to the speed after tadpole deposition had occurred. As has been shown in another
472 poison frog species (Smith et al., 2006), the presence of tadpoles does not seem to inhibit the
473 locomotory performance of transporting frogs. We assume that overall costs during tadpole
474 transport are higher than during homing, as the survival of the transported offspring also has to
475 be accounted for. As a result, frogs appear to adjust their movements and, for instance, quickly
476 deposit their offspring to prevent the tadpoles from drying out (Downie et al., 2005). However,
477 why frogs are slower during homing still remains unclear. Since frogs do not appear to explore
478 during homing, faster homing should reduce the risk of losing mating opportunities (Roithmair,
479 1992; Ringler et al., 2013), or even the entire territory. Potential exhaustion after tadpole
480 deposition, time needed for homewards orientation or high risk of predation during fast
481 movement might explain slower movement during homing, but future studies need to examine

482 these factors in more detail. All movements were in general characterized by stop-and-go phases
483 of varying duration and speed. Intermittent movement patterns can be found in many organisms
484 ranging from protozoans to mammals, and in a variety of behavioral contexts such as searching
485 or habitat assessment. Frequent stops could lead to perceptual benefits because animals then have
486 time to scan the area, and conspicuousness towards predators might be reduced (Kramer &
487 McLaughlin, 2001). Hence, the stop-and-go locomotion pattern of male frogs during tadpole
488 shuttling and homing could be a further adaptation for orientation and resting, while reducing
489 risks related to continuous movement.

490

491 Pool visits

492 During the entire study, we never observed male frogs that encountered a removed artificial or
493 dry natural pool exhibiting any exploratory behavior after the deposition of tadpoles. Two
494 individuals that encountered an unavailable deposition site were observed during a second
495 tadpole transport event when they visited the very same unavailable pool. In contrast to our
496 predictions, the actual availability of potential deposition sites had little influence on the
497 movement patterns of male frogs, and no apparent updating of information concerning resource
498 availability during tadpole transport occurred. In our study, all frogs except one (which lost
499 tadpoles overnight) managed to find an available pool for deposition even if they had previously
500 encountered a removed or dry pool. Furthermore, we recorded one male visiting a natural pool
501 site that never held water during the entire study period and could only have been known as a
502 potential deposition site from previous years. These findings suggest that male frogs rely
503 predominantly on their spatial memory to find deposition sites and do not invest time and energy
504 in exploring further pools during tadpole transport. The availability of suitable breeding pools

505 can change rapidly in the tropics as a result of sudden, heavy rainfalls or fast desiccation due to
506 strong solar radiation. Nevertheless, resource availability seems to be sufficiently stable for frogs
507 to rely on memory-based orientation strategies. Previously unavailable pools might turn into
508 available breeding resources after one heavy rainfall, whereas some pool locations remain the
509 same not only for the entire breeding season, but for several years at a time. Thus, frogs may
510 remember previously visited pools as having been available in the past and to be at least in
511 principal able to contain water. The best strategy might be to remember previous sites and visit
512 them repeatedly, even at the risk that they might have vanished since the last visit. Many nectar-
513 feeding species use similar strategies and primarily use spatial information to relocate flowers
514 over object-based cues (e.g., Hurly & Healy, 2002; Thiele & Winter, 2005; Carter, Ratcliffe &
515 Galef, 2010). In a study on nectar-feeding bats (*Glossophaga commissarisi*) they could show that
516 flight approaches to feeders that were primarily guided by spatial memory were of shorter
517 duration than approaches that included object-based cues, indicating that there is a short-term
518 energy advantage to the spatial-memory strategy (Thiele & Winter, 2005). Relying primarily on
519 spatial memory to find pools repeatedly is probably also more efficient than locating them based
520 on goal-associated cues.

521

522 We did not find any difference when comparing the precision and speed of frogs that moved
523 towards an available or unavailable deposition site, suggesting that pool-associated cues, such as
524 odor, do not play a major role in orientation towards the pools. This further supports evidence
525 that *A. femoralis* mainly uses suitable pools based on spatial memory (Pašukonis et al., 2016).
526 Olfaction, however, has been shown to play a role in poison frog pool choice (*R. variabilis*;
527 Schulte et al., 2011 and Schulte & Lötters, 2014) and orientation (*A. femoralis*; Pašukonis et al.,

528 2016). In *A. femoralis* olfactory cues might especially play a role in the initial discovery and
529 evaluation of suitable deposition sites. Finally, other indirect cues, such as pool-associated
530 microhabitat (e.g., as in salamanders (Jenkins, McGarigal & Timm, 2006)) or calls of
531 heterospecifics (e.g., as in newts (Diego-Rasilla & Luengo, 2007)), might be used by tadpole-
532 transporting frogs to discover breeding sites. For example, transporting males of the poison frog
533 *Dendrobates tinctorius* were found to gather at sites of fresh treefalls, which often provide new
534 deposition sites (Rojas, 2015).

535 Recent tracking and genetic studies have revealed that *A. femoralis* remember the location of up
536 to six different pool sites (Pašukonis et al., 2016) and that frogs actively partition their offspring
537 across several water bodies as a possible reproductive bet-hedging strategy (Erich et al., 2015).
538 Our results corroborate these findings as tracked individuals usually visited and used two to three
539 deposition sites per tadpole transport event. Most frogs moved considerable distances beyond the
540 boundaries of their territory and often used pools that were not the closest ones to their territory.
541 However, we cannot entirely rule out that some of the movements we observed between multiple
542 pool sites were a byproduct of disturbance from tracking and handling. If tadpole distribution
543 over several sites improves offspring survival, then knowing more pool locations should have
544 direct fitness consequences. We speculate that this creates a trade-off between minimizing the
545 costs of tadpole transport and maximizing the potential benefits gained through offspring
546 partitioning over multiple learned sites (see Erich et al., 2015).

547

548 **Conclusions**

549 While it remains unknown when and how the poison frog *A. femoralis* collects information about
550 the surrounding area, we provide, for the first time, detailed information about the movement

551 patterns during tadpole transport. We observed highly directional movement between territories
552 and pools as well as between pools, suggesting an advantage of quick tadpole transport and
553 homing over additional detours to explore the area. Future research should investigate in more
554 detail the costs and benefits of tadpole transport in order to understand the trade-offs shaping
555 movement strategies in such dynamic environments. Further, the mechanisms that allow poison
556 frogs to establish a spatial memory and orientate with such high precision in the rainforest
557 remain unknown.

558 Despite extensive capture-recapture studies (e.g., Brown, Morales & Summers, 2009; Ringler,
559 Ursprung & Hödl, 2009), and some tracking of *A. femoralis* after translocations (Pašukonis et al.,
560 2014a,b) and tadpole transport (Pašukonis et al., 2016), still very little is known about the natural
561 movement patterns of poison frogs and tropical amphibians in general. Tropical amphibians
562 exhibit a huge diversity in breeding strategies ranging from explosive breeders that gather in
563 ponds to prolonged breeders that depend on widespread, ephemeral pools for tadpole
564 development. This diversity and the dependence on water bodies for reproduction make tropical
565 amphibians a valuable study system to investigate how animals deal with varying resource
566 availability and how this shapes movement patterns. Our findings contribute to the knowledge of
567 spatial behavior in poison frogs and will hopefully encourage further research on movement
568 ecology of tropical amphibians.

569

570

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577

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Figure 1

Map of the study area

Experimental setup and the distribution of male territories in the study area. Red asterisks represent the center of tracked frog territories ($n=16$) and white asterisks represent the territory centers 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.

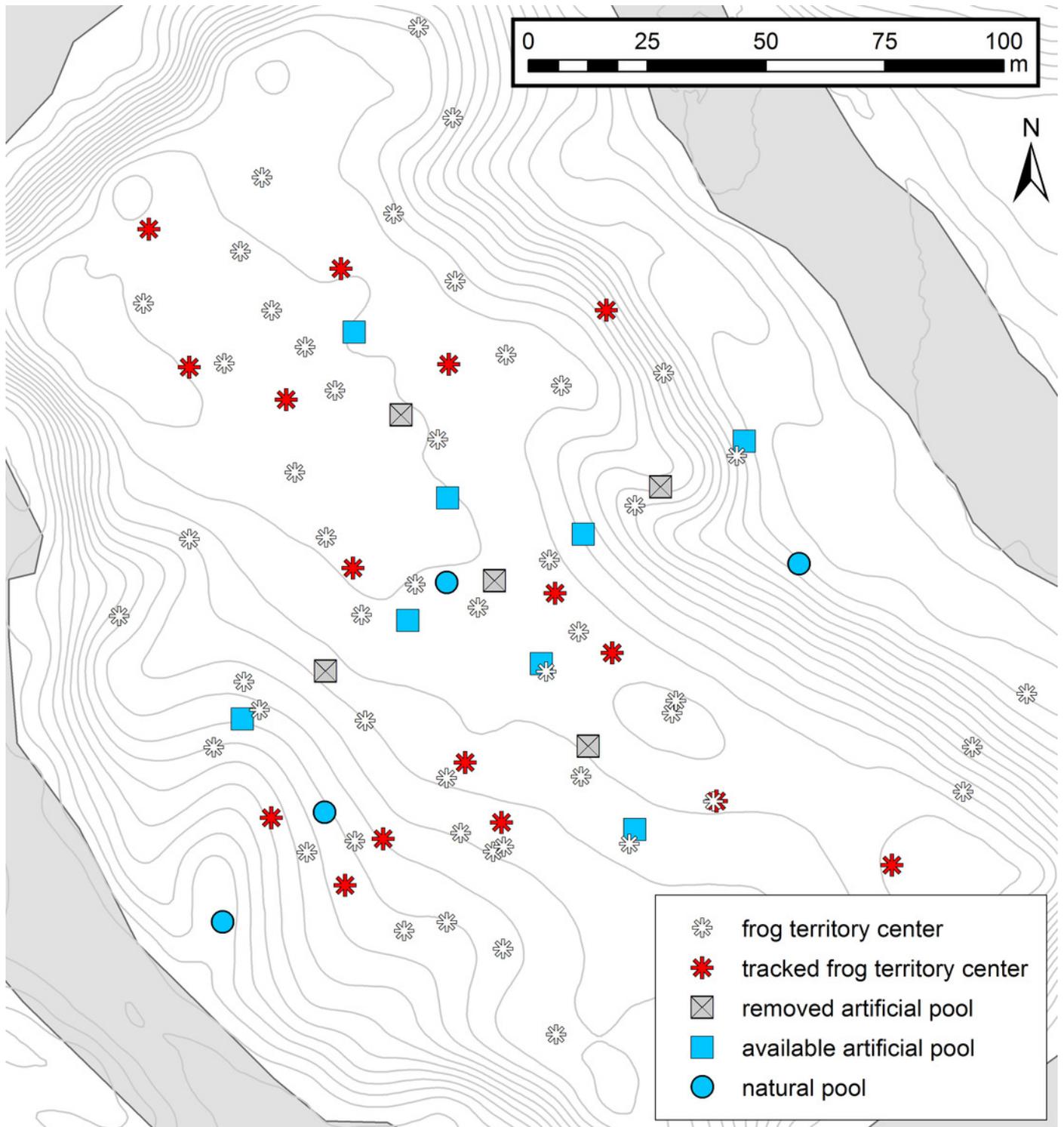


Figure 2

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.

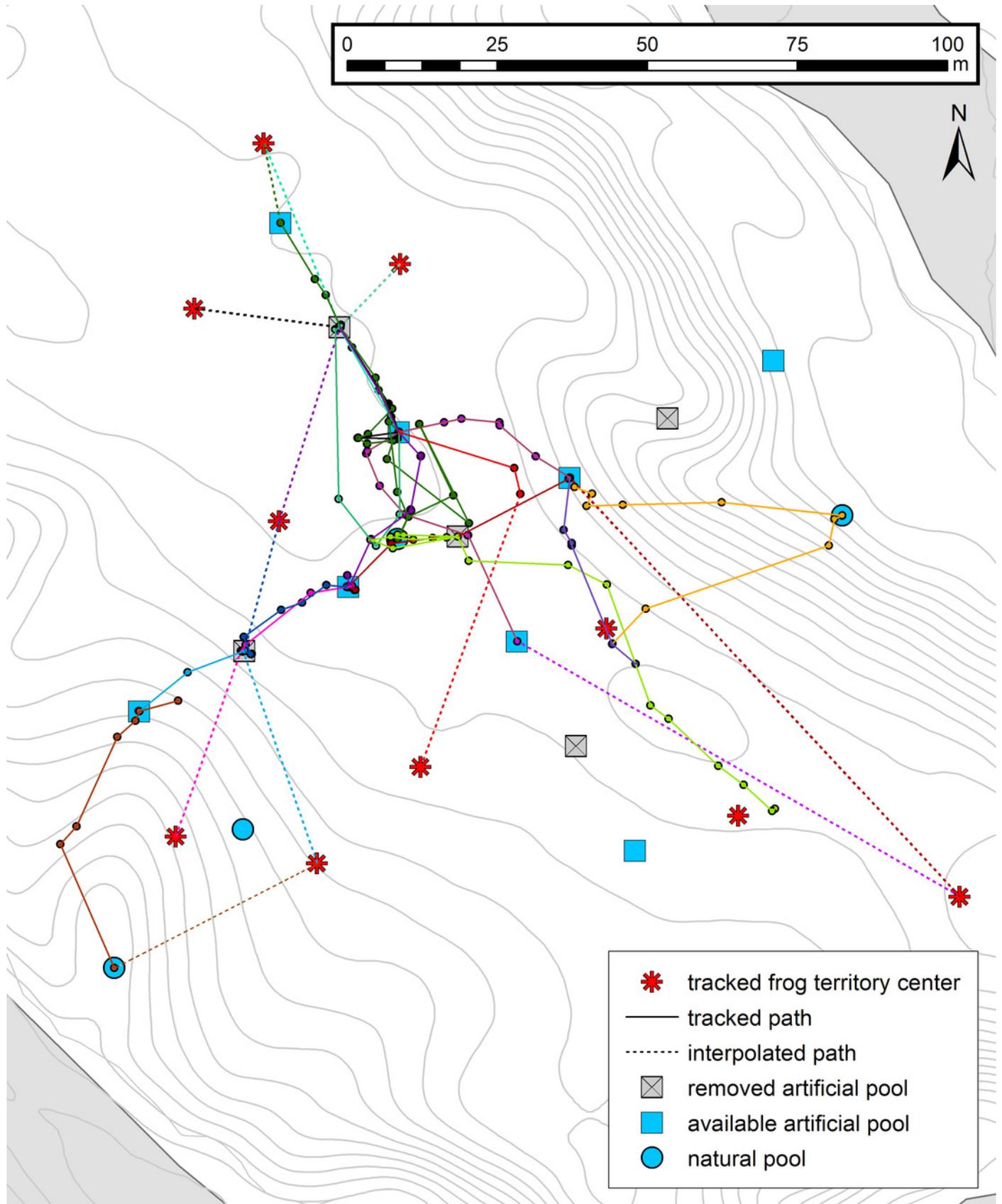


Figure 3

Movement speed during tadpole transport and homing

Boxplot showing the average speed (m/h) for the TTs and HTs.

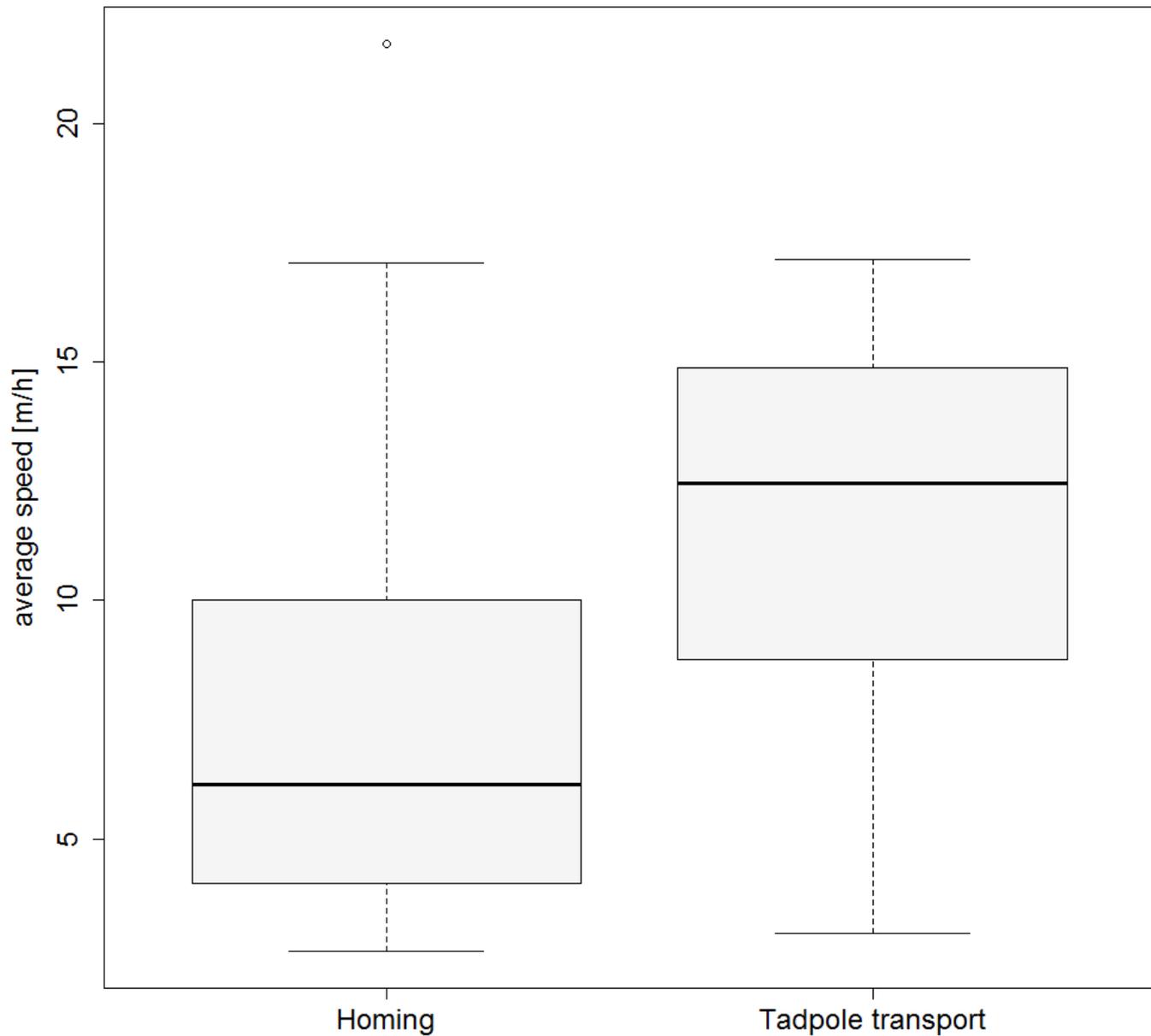


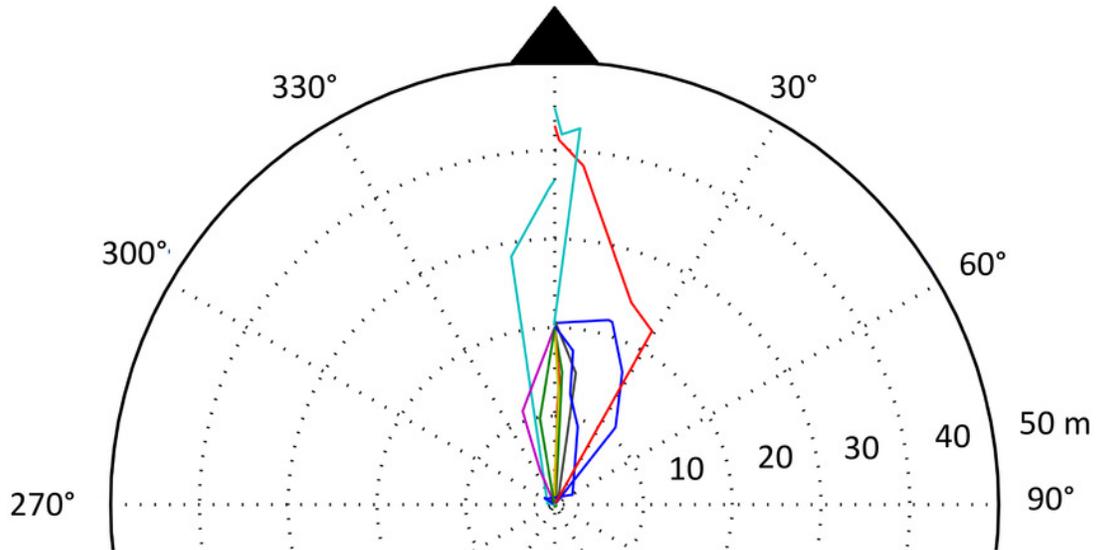
Figure 4

Tadpole transport and homing trajectories

Part of a polar plot showing A) the tadpole transport (TT) and B) homing (HT) trajectories of male *A.femoralis*. Each colored line represents one trajectory (TT: n = 11, 7 individuals; HT: n=22, 16 individuals). For better visualization, we only plotted the parts of TTs showing the movement between the first two pool sites visited. TTs that did not pass by at least two pool sites are excluded from the plot. All trajectories were normalized to a single starting point (center of the plot), which corresponds to the first pool visited for the TTs and to the last deposition site for the HTs. The full extent of the plot corresponds to 50 m for TTs and to 100 m for HTs.

A

Tadpole transport

**B**

Homing

