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Take the long way home: Behaviour of a neotropical frog, *Allobates femoralis*, in a detour task

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Abstract

Detour behaviour, an individual's ability to reach its goal by taking an indirect route, has been used to test spatial cognitive abilities across a variety of taxa. Although many amphibians show a strong homing ability, there is currently little evidence of amphibian spatial cognitive flexibility. We tested whether a territorial frog, *Allobates femoralis*, can flexibly adjust its homing path when faced with an obstacle. We displaced male frogs from their calling sites into the centre of circular arenas and recorded their escape routes. In the first experiment we provided an arena with equally high walls. In the second experiment we doubled the height of the homeward facing wall. Finally, we provided a tube as a shortcut through the high wall. In the equal-height arena, most frogs chose to escape via the quadrant facing their former calling site. However, when challenged with different heights, nearly all frogs chose the low wall, directing their movements away from the calling site. In the "escape tunnel" experiment most frogs still chose the low wall. Our results show that displaced *A. femoralis* males can flexibly adjust their homing path and avoid (presumably energetically costly) obstacles, providing experimental evidence of spatial cognitive flexibility in an amphibian.

Keywords

Amphibian behaviour; Spatial cognitive flexibility; Dendrobatidae; Homing; Obstacle avoidance

1 Introduction

Survival and reproductive success depend on an animal's ability to efficiently find its way through the habitat towards resources such as food, water, mating partners and shelter. Most animals live in complex habitats containing irregular terrain and structures that block the direct path. An animal must be able to flexibly over-come such obstacles in order to reach its objectives (Kohlsdorf and Biewener, 2006), even if that involves increasing its distance from, or giving up direct sight of, the goal (Tarsitano, 2006; Zucca et al., 2005).

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Detour behaviour studies were pioneered by Köhler (1999) who showed that chimpanzees, dogs and chicks could reach their target by going around physical barriers. Detour studies have since been used to study behavioural plasticity in other mammals (Baragli et al., 2010; Chapuis and Varlet, 1987; Chapuis et al., 1983; Kimchi and Terkel, 2003; Nesterova and Hansen, 2009; Poucet et al., 1983; Smith and Litchfield, 2010; Wynne and Leguet, 2004), birds (Regolin et al., 1995, 1994; Zucca et al., 2005), reptiles (Lustig et al., 2013), arachnids (Tarsitano and Jackson, 1994, 1997; Tarsitano, 2006) and insects (Collett, 1996). Most detour tests are performed in artificial laboratory conditions and test an animal's ability to detour when the goal is represented by food (Regolin et al., 1995; Tarsitano and Jackson, 1994; Tarsitano, 2006; Wynne and Leguet, 2004) or social reward (Bisazza et al., 1997; Regolin et al., 1995; Zucca et al., 2005). Many amphibians naturally show long distance goal directed movements to breeding or home sites (Sinsch, 2014). Although the sensory basis of spatial orientation has been studied in several anuran species, very little is known about the flexibility involved in their way-finding (but see Collett, 1982; Ingle, 1973, 1970; Lock and Collett, 1980, 1979). Green toads (*Pseudepidalea viridis*) are able to take a detour around a semi-transparent fence to reach food, but apparently are unable to compare different path lengths, and take routes even if they have a visible obstacle further along the path (Collett, 1982).

Poison frogs (Dendrobatidae) display some of the most complex spatial behaviours known among amphibians, such as territoriality and tadpole transport. The brilliant-thighed poison frog (*Allobates femoralis*) is a small leaf litter species common throughout the Amazon basin and the Guiana Shield (Amézquita et al., 2009). Males defend long-term territories that they use as feeding grounds and mating sites (Narins et al., 2003; Ringler et al., 2012, 2009; Roithmair, 1992). Males produce advertisement calls from fixed calling sites (i.e. elevated structures above the forest floor) within their territories (Ringler et al., 2009). Like many dendrobatid frogs, male *A. femoralis* shuttle tadpoles from their territories to widely distributed aquatic deposition sites (Ringler et al., 2013). Experimentally translocated males return to their territories from up to 400 m in just a few days (Pašukonis et al., 2013) following a direct path (Pašukonis et al., 2014a, 2014b).

We conducted a field experiment to examine the way-finding flexibility of male *A. femoralis* in a detour task. More specifically, we analysed the escape routes of territorial males translocated from their calling sites to an enclosed circular arena. We hypothesized that translocated males would: 1) escape by jumping over the arena wall towards its former calling site, given an equal-height arena, 2) take a detour by jumping over the lower part of the wall, if a higher wall was facing the calling site and 3) prefer a straightforward path homeward, if available.

2 Material and Methods

2.1 Study animals and location

We studied individual frogs from an *A. femoralis* population near the 'Saut Pararé' field camp (4°02'N, 52°41'W, WGS84) of the Nouragues Ecological Research Station (www.nouragues.cnrs.fr), in the nature reserve 'Les Nouragues', French Guiana. We carried out the study between 4th and 14th of February 2013, and the trials were performed between

10:00–18:30. This period marked the beginning of *A. femoralis* mating season when males were calling throughout the day and were motivated to return to their former calling site after displacement.

We captured 35 calling males, which were identified as territorial if they showed positive phonotaxis to a playback of a simulated male intruder. To avoid retesting the same frog, we identified frogs by their individual ventral patterns and noted the location of its calling site on a digital map (Ringler et al., 2014) using pocket computers (MobileMapper™ 10, Spectra-Precision, Westminster, Co., USA) with the ArcPad™ 10.0 (ESRI, Redlands, CA, USA) geographic information system. Promptly after capture we translocated the frogs a mean \pm SE distance of 7.4 ± 0.78 m (range: 2–20 m) away from their calling sites, to a portable experimental arena, placed near that male's home range. Each individual was naive in respect to the arena setup and was only tested once.

2.2 Experimental setup and procedure

The mobile circular arena ($\varnothing = 100$ cm) was made out of dark green plastic walls and a black plastic base. We marked the angles of the arena clockwise, in 22.5° incremental steps, on the plastic floor surface, outside of the arena. On location, we fixed the arena with two metal poles attached to the outer perimeter of the walls, and always oriented the 0° angle towards the translocated subject's original calling site (Fig. 1B).

We placed the subject in the centre of the arena under a releasing device consisting of an inner opaque wooden cup ($\varnothing = 6$ cm) and an outer transparent bottle ($\varnothing = 8$ cm) that could be lifted using a string run through a modified tripod above the arena (Fig. 1A). We kept each frog for two minutes under the opaque cup to habituate. We then allowed the frog a five-minute "orientation phase" under the transparent bottle with the opaque cup lifted, to avoid random escape behaviour. Subsequently, we lifted the entire releasing device and allowed the individual a "locomotory phase" of maximum 120 min to escape the arena. We counted a trial as completed once the frog touched the ground outside the arena. If the frog spent more than 120 min within the arena without escaping, we halted the trial and released the frog; such trials were coded as incomplete. Once outside the arena, we attempted to follow the frogs' movement direction, keeping a distance of approximately 3 m to avoid disturbing the individual. However, frogs were sometimes lost out of sight after a short distance due to the difficult observation conditions (small dark frog in low light forest understory) or when frogs hid behind forest floor structures (e.g., leaves, logs, roots).

We video-recorded the trials using a tripod-fixed camera filming from an elevated angle. Two experimenters, that were positioned 3 m away from the arena and in opposing angles, noted additional information on the frequency of movements, escape angle and strategy. We applied three consecutive test conditions to different frogs, respectively. In an equal-height arena test we assessed the choice of the escape route in relation to the calling site direction, by providing equally difficult escape possibilities from the arena at all angles, i.e. 20 cm high uniform walls ($n = 11$). We chose the wall height to be high enough that the frogs would not see their calling sites directly but low enough that the frogs would be able to jump over it. In an unequal-height obstacle arena test, we confronted 10 further individuals with a higher wall facing their calling site. For this purpose, we raised this semi-circular section of

the wall to a height of 36 cm, while leaving the other half at 20 cm (Fig. 1A). During pilot trials we determined that frogs would not be able to jump over a wall of 36 cm but they could climb over it if no other escape possibility was available. We always rotated the centre of the high wall to 0° towards the initial calling location of the tested individual. Finally, in a third test we provided an additional escape route and tested 10 further individuals. For this, we fitted an arena identical to the unequal-height condition with a grey plastic tube ($\varnothing = 7$ cm) located at the centreline of the high wall, elevated 5 cm from the ground. Oriented at 0°, the tube provided a straightforward but narrow (snout-vent length of these frogs is approximately 3 cm) shortcut towards the focal individual's specific calling site.

2.3 Data analysis

Of 35 initiated trials, we excluded four trials from our analysis: three from the first test (in one case because heavy rain flooded the arena, in another case a branch, fallen during the experiment, provided an additional escape route, in one case the frog escaped underneath the arena wall), and one incomplete trial from the second test, when the subject did not manage to escape within the allocated maximum time.

This left 31 valid escape trials, which were coded from the video footage. During the locomotion phase we scored all movements, such as: hops, jumps, pivotal body orientations and wall climb attempts. For each frog, we summed the number of such movements, and also calculated the total time spent in the arena.

For statistical analysis, we measured the variation in the angles about the mean direction with a V-test for circular uniformity (with expected mean directions of 0° in the equal-height arena and of 180° in the unequal-height arena) in the circular statistics software Oriana v. 4.02 (Kovach Computing Services, Pentraeth, Wales, UK). In addition, we used the Oriana software to calculate the correlation coefficient between the escape angle and both movement and time spent in the arena using the circular-linear correlation.

Because of the wide spread of the mean vectors, we further tested for homeward escape in the standard arena with a Chi-squared test on quadrant grouped escape angles. All linear statistics were done with SPSS 20.0.

3 Results

Frogs escaped the arena either by climbing up the wall, or by jumping onto the edge of the wall and then outside, or by a combination of jumping and climbing. We found no significant difference in time spent in the arena (Kruskal-Wallis test: $H = 3.45$, d.f. = 2, $p = 0.178$) or number of movements (Kruskal-Wallis test: $H = 1.58$, d.f. = 2, $p = 0.454$) across the three experimental conditions. We also found no correlation between time spent in the arena and the escape angle (Spearman's $\rho = 0.099$, $p = 0.603$), or movement frequency and escape angles (Spearman's $\rho = -0.35$, $p = 0.854$). However, time spent in the arena and number of movements was correlated (Spearman's $\rho = 0.654$, $p < 0.000$): unsurprisingly, frogs that took longer to escape also made more movements in the arena.

3.1 Equal-height arena test

When faced with a uniform height of the arena wall, the frogs predominantly chose an escape path towards the calling site (Mean = 7.2° , 95% CI = 306.5° – 67.9° , V-Test $p = 0.024$, $n = 11$). Out of the 11 individuals, 7 escaped via the 90° -quadrant facing towards the calling site, which differs significantly from a uniform random choice ($\chi^2 = 9$, d.f. = 3, $p = 0.029$, Fig. 2A). Thus, all things being equal, frogs chose to escape in the direction of their former calling site.

3.2 Unequal-height obstacle arena test

However, when confronted with a high wall facing their initial calling site, the majority of the frogs ($n = 9$ out of 10) avoided the higher obstacle and instead escaped via the lower wall. One individual climbed over the high wall (Mean = 199.1° , 95% CI = 148.7° – 249.5° , V-Test $p = 0.016$, $n = 10$) ($\chi^2 = 6.4$, $p = 0.011$, Fig. 2B), showing that escape over the higher wall was physically possible. Once outside the arena, out of 9 frogs that escaped over the low wall, 7 readjusted their trajectory towards their former calling site, while the other 2 individuals moved away in different directions.

3.3 Unequal-height obstacle arena test with escape tunnel

In the arena test with an additional escape tunnel, frogs predominantly climbed over the low wall ($n = 6$), while only three frogs used the escape tunnel ($\chi^2 = 3.8$, $p = 0.150$, Fig. 2C). Again one individual climbed the high wall facing homeward. Outside the arena, out of 6 frogs that escaped over the low wall, 4 readjusted their trajectory towards their former calling site, while 2 went in different directions.

4 Discussion

We found that male *A. femoralis* preferred to escape towards their former calling site when placed in an arena with uniform wall height. However, when confronted with a higher wall facing the calling site, frogs mostly chose to detour by jumping over the lower wall. They continued to prefer this “detour escape” even in the presence of an additional shortcut passage facing directly towards their initial calling site.

As expected, the former calling site seems to be a powerful motivator for *A. femoralis* and a reliable objective in a detour task comparable to food for jumping spiders (Tarsitano and Jackson, 1994) or green toads (Collett, 1982), and social rewards for chicken (Regolin et al., 1995). Frogs appear to be capable of avoiding potentially energetically expensive obstacles. However, this task was not physically inevitable: the higher obstacle was not impossible to overcome, as shown by two individuals who chose to escape over the higher wall towards their former calling site, further supporting the results from the arena with equally high walls. Also, almost half of the tested frogs immediately went towards their former calling sites, touched the wall repeatedly, and looked up before deciding where to escape. Interestingly, the majority of the tested males seemed to “evaluate” the situation. They stayed in the centre of the arena while turning or hopping in different directions, and then escaped over the low wall on the first try, suggesting a strategic avoidance of the higher obstacle. In hindsight, an equal-height arena with high walls (i.e. 36 cm) would have been a

valuable additional control to assess frogs' ability and motivation to choose the homeward direct escape route, without an alternative route available. However, with limited time in the field and limited knowledge of *A. femoralis* jumping capabilities, we chose the low wall as a safer and still informative control condition.

Contrary to our expectations, the majority of individuals from the third test did not choose the tunnel as an escape route. In an earlier study, green toads (*P. viridis*) predominantly used the shortcut through an obstacle, but this was represented by a simple gap in a palisade (Collett, 1982). This difference might be due to the fact that frogs in our arena did not have a direct sight of the calling perch through the elevated tunnel. Without the direct sight outside, the confined tunnel might have not appeared as a valid or safe escape route to the frogs.

Our results on homeward escape orientation are in line with a previous study that demonstrated the striking ability of males of this species to take a direct trajectory to return to their territory after being translocated up to 360 m (Pašukonis et al., 2014b). However, in another study the authors did not find an initial homeward orientation in a similar arena setup when relocating frogs over a short distance (<35 m) from their territory (Pašukonis et al., 2014a). In our study we found that translocating *A. femoralis* males over a mean distance of seven metres from their calling site leads to the majority of frogs choosing to escape towards their former calling site. We additionally observed that most individuals that did not escape directly towards home, readjusted their movement once outside the arena, and then headed towards their former calling site. A few individuals did not immediately home back, but hid in the leaf litter after their escape. These individuals might not have been motivated to call again after the trial and thus did not show immediate orientation towards the calling site. Given that *A. femoralis* males of the study population occupy territories averaging 14 m in diameter, and territory size varies largely between individuals (Ringler et al., 2011; Roithmair, 1992) it is likely that, in many cases, our arena was set up within the focal male's defended and safe area. In general, the tested subjects were seen calling in their territory during the next days.

Previously, amphibian detour behaviour has been documented only under laboratory conditions (Collett, 1982; Lock and Collett, 1979). Our study represents an attempt at an experimental demonstration of anuran detour behaviour in the field. We found that *A. femoralis* males are capable of avoiding obstacles in a detour task in their natural habitat towards reaching an ecologically relevant goal—their calling site. Poison frog ecology involves territory defense, tadpole transport and calling site selection in a dynamic environment, the rainforest, and consequently demands a degree of way-finding flexibility. Together with several recent studies on *A. femoralis* (Pašukonis et al., 2014b; Ringler et al., 2015) our results address the incomplete picture of spatial cognitive flexibility in amphibians. Our study introduces the use of translocation and portable arenas as a simple new method suitable for studying amphibian behavioural plasticity in the field—a topic that merits further investigation.

Appendix A. Supplementary data

Refer to Web version on PubMed Central for supplementary material.

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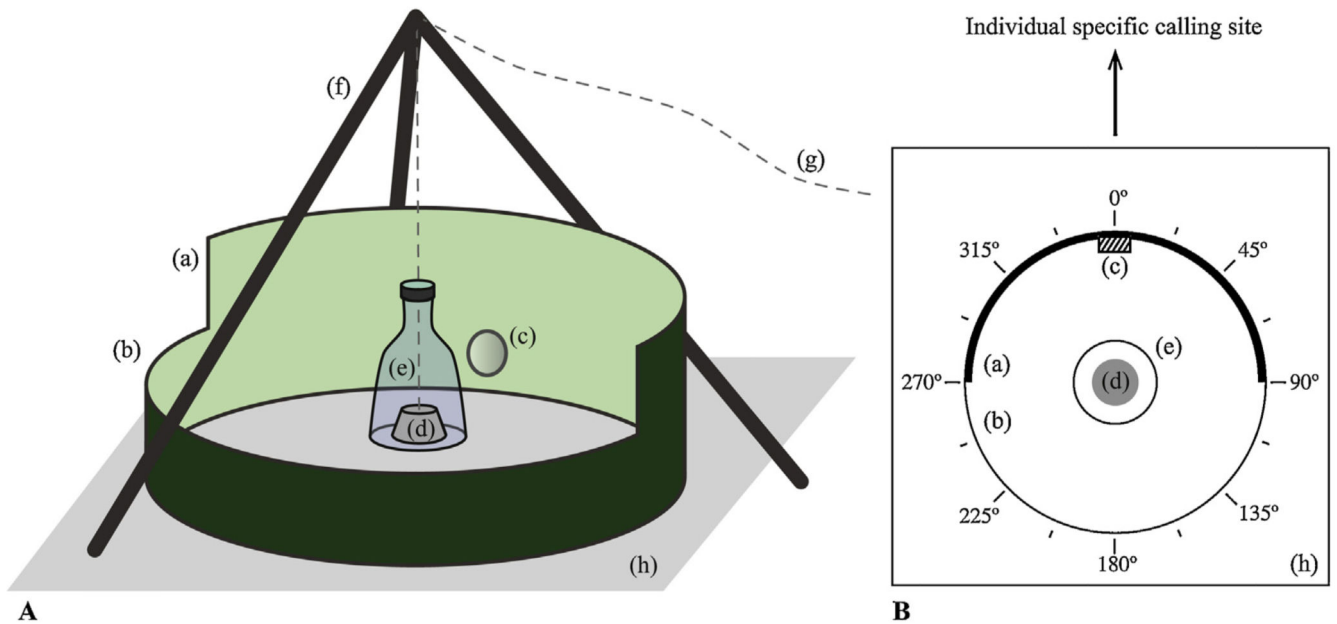


Fig. 1. Schematic representation of unequal-height arena with escape tunnel (condition three).

A. Lateral view. B. Aerial view. The arena is composed of: (a) high wall, (b) low wall and (c) escape tunnel. The release device is composed of: (d) opaque cup, (e) transparent bottle, (f) modified tripod and (g) string. The arena floor (h) has angles marked in 22.5° increments. The arena was always positioned with starting angle (0°) pointing towards the focal individual's specific calling site.

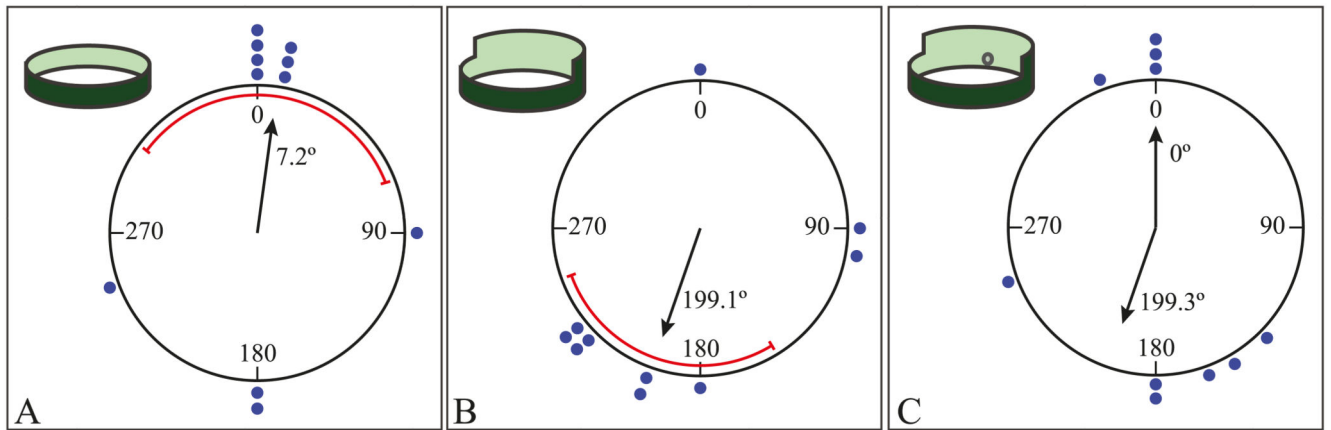


Fig. 2. Results of the arena experiments.

A. Equal-height arena test. B. Unequal-height arena test. C. Unequal-height arena test with escape tunnel. Outer points represent escaped individuals and are placed at the corresponding escape angle; arrows represent the mean escape angle; and arc segments represent the 95% confidence interval. In the last experiment, the two arrows indicate the escape angle for three tunnel escapees (0°) and the mean escape angle for the over-the-wall escapees (199.3°).