The Company of Biologists

SHORT COMMUNICATION

Map-like navigation from distances exceeding routine movements in the three-striped poison frog (*Ameerega trivittata*)

Andrius Pašukonis[1],[*],[‡], Matthias-Claudio Loretto[1],[*] and Walter Hödl[2]

ABSTRACT

Most animals move in dense habitats where distant landmarks are limited, but how they find their way around remains poorly understood. Poison frogs inhabit the rainforest understory, where they shuttle tadpoles from small territories to widespread pools. Recent studies revealed their excellent spatial memory and the ability to home back from several hundred meters. It remains unclear whether this homing ability is restricted to the areas that had been previously explored or whether it allows the frogs to navigate from areas outside their direct experience. Here, we used radio-tracking to study the navigational performance of three-striped poison frog translocated outside the area of their routine movements (200–800 m). Translocated frogs returned to their home territory via a direct path from all distances and with little difference in orientation accuracy, suggesting a flexible map-like navigation mechanism. These findings challenge our current understanding of both the mechanisms and the sensory basis of amphibian orientation.

KEY WORDS: Amphibians, Homing, Map navigation, Telemetry, Spatial orientation

INTRODUCTION

The ability to flexibly choose the direct path from arbitrary release points to goals outside direct sensory contact is considered a hallmark of a map-like navigation mechanism (Jacobs and Menzel, 2014; Pritchard and Healy, 2017). Under natural conditions, navigational flexibility has been mostly studied in birds flying over tens or hundreds of kilometers and in insects moving over tens or hundreds of meters (reviewed in Jacobs and Menzel, 2014). Very different underlying mechanisms have been typically implicated to explain navigational flexibility at different scales. At large scales, animals rely on extended gradients or directional cues such as odor or magnetic field, which can provide a general directional or positional information (Lohmann et al., 2007; Wallraff, 1980; Wiltschko and Wiltschko, 2009). At small scales, animals often use spatial learning, route following, distant visual landmarks and small-scale guidance strategies, which require at least partial familiarity and direct contact with the local cues (Cheng and Jeffery, 2017; Pritchard and Healy, 2017). Most animals, however, routinely move at an intermediate scale and in highly structured habitats, where many distant cues are limited. How animals in these habitats find their way around and the flexibility of their navigation remain poorly understood.

Quantifying detailed movement patterns after experimental displacements is key in studying animal orientation, but tracking small animals moving in densely vegetated environments, such as the forest understory, remains challenging. Amphibians and reptiles are ubiquitous in such densely vegetated habitats, especially in the tropical regions. When compared with other small vertebrates, amphibians are relatively slow and sedentary, making them a more accessible system for understanding how animals find their way around in such complex environments. Tropical amphibians show a diversity of reproductive and spatial strategies, but research on spatial orientation has focused almost exclusively on nocturnal, pond-breeding amphibians of temperate regions (reviewed in Ferguson, 1971; Sinsch, 1992; Sinsch, 2006). The ability of some amphibians to return after translocation from hundreds of meters or even kilometers has been known for decades (e.g. Bogert, 1947; Jameson, 1957; Matthews, 2003; Twitty et al., 1964). At least two newt species have been shown to orient from unfamiliar release sites (Fischer et al., 2001; Phillips et al., 1995; Twitty et al., 1964, 1967), suggesting the use of a large-scale gradient (grid navigation *sensu* Papi, 1990). Other species of newts (Sinsch and Kirst, 2016), frogs (Dole, 1968; Oldham, 1967) and toads (Sinsch, 1987) have failed to predictably orient with increasing translocation distance, which has been used to argue that homing of most amphibians is restricted to areas directly explored in the past (Sinsch, 2006; Sinsch and Kirst, 2016). The underlying homing mechanisms and the degree of navigational flexibility, however, are not known for any amphibian. The importance of certain sensory modalities, such as olfaction and magnetoreception, has been revealed for a few species (e.g. Fischer et al., 2001; Ishii et al., 1995), but the homing trajectories have rarely been quantified, and thus it remains unknown whether the use of these cues can explain the orientation behavior observed in the field.

Poison frogs (Dendrobatidae) are small Neotropical rainforest frogs with complex spatial behavior. Most species are terrestrial and defend long-term territories on the forest floor, where mating occurs. Tadpoles develop on land until one of the parents transports them on their back to suitable aquatic nurseries (Wells, 2007; Weygoldt, 1987). The ability to home back after translocations has been demonstrated in several poison frog species (Nowakowski et al., 2013; Pašukonis et al., 2013; Pichler et al., 2017), but the sensory and spatio-cognitive mechanisms underlying this ability remain unknown. Recent tracking studies revealed that territorial males of the poison frog *Allobates femoralis* can return to their territory via a direct path after translocations of up to 400 m. The frogs are disoriented when translocated to an unfamiliar area across a river barrier, suggesting that some experience with the local cues is necessary for navigation (Pašukonis et al., 2014a). Recent evidence has also shown that spatial learning plays a key role in this species' ability to find the pools for tadpoles (Beck et al., 2017; Pašukonis

[1]University of Vienna, Department of Cognitive Biology, Althanstrasse 14, Vienna 1090, Austria. [2]University of Vienna, Department of Integrative Zoology, Althanstrasse 14, Vienna 1090, Austria.
*These authors contributed equally to this work

‡Author for correspondence (andrius.pasukonis@univie.ac.at)

A.P., 0000-0002-5742-8222; M.-C.L., 0000-0002-1940-3470; W.H., 0000-0002-1990-9682

et al., 2016). Paradoxically, extensive exploration or movements longer than 200 m have not been observed in *A. femoralis*, and recorded movements rarely exceed 100 m (Beck et al., 2017; Ringler et al., 2009, 2013). The disparity between observed homing distances and the range of natural movements might indicate that frogs can extrapolate the learned cues and use them for navigation outside the range of their routine movements. Detailed data on movement patterns after translocations to incrementally increasing distances are necessary before further hypotheses about the mechanisms underlying poison frog navigation can be formulated. Here, we studied the navigational performance of male three-striped poison frogs [*Ameerega trivittata* (Spix 1824)] translocated outside the presumed area of their routine movements.

MATERIALS AND METHODS
Study species and study site
The data were collected around the onset of the rainy season from 15 October to 18 November 2014, at the Panguana Biological Field Station inside the 'Área de Conservasión Privada Panguana' on the lower Río Llullapichis, Amazonian Peru (9°35′S, 74°48′W). The study area consists of lowland rainforest with a moderate relief, intersected by several creeks, and bordering a pastureland on one side (Figs S1 and S2). *Ameerega trivittata* is one of the largest (average male snout–urostyle length=39 mm, average male mass=5.5 g) and most widely distributed dendrobatid frogs (http://amphibiaweb.org). It is one of the few dendrobatid frogs sufficiently large enough to carry radio transmitters allowing long-distance tracking. Males vocally advertise and defend territories on the forest floor (territory size up to 156 m^2; see Roithmair, 1994), where courtship and oviposition take place. After approximately 18 days of larval development, males transport up to 41 tadpoles to pools and creeks usually outside their territory (Luiz et al., 2015; Roithmair, 1994). Like most dendrobatid frogs, *A. trivittata* are diurnal.

Tracking and experimental procedure
We scanned the area for calling males during the morning peak calling time (Roithmair, 1994). We used individual coloration patterns for identification, and males were considered territorial if they were observed calling in the same area on at least two different days. From 15 October to 5 November, 24 males were captured and equipped with a short-range tracking device (harmonic-direction finder; for details, see Mascanzoni and Wallin 1986; Pašukonis et al., 2014b) and released for an observation period of 1–7 days. During this period, we located the frogs one or two times a day and observed their territorial behavior and local movements. We also recaptured and shortly handled the tagged frogs one or two times during this period to check the fit of the waistband. Tags were removed if any signs of skin-wear (*n*=5) or extensive hiding periods (*n*=4) were noticed. Of the remaining frogs, 12 territorial males were re-equipped with miniature radio transmitters (BD-2X from Holohil Systems Ltd, Carp, ON, Canada, and NTQ-2 from Lotek Wireless Inc., Newmarket, ON, Canada), which were attached externally, using thin medical quality silicone tubing (Fig. S3). The total tag mass was 0.38–0.5 g compared with the male mass of 4.5–6.8 g. Radio-tagged frogs were translocated 203–792 m (mean=476 m) away from their territory northwards or southwards (Fig. S2). Single individuals were placed in an airtight opaque container (Fig. S4), rotated multiple times and brought to the release site by an indirect path. Not more than two individuals were translocated on the same day. After release, the frogs were tracked four to six times a day during daylight hours using a portable radio-tracking receiver (Sika,

Biotrack Ltd, Wareham, Dorset, UK) and a flexible Yagi-antenna (Biotrack Ltd). When possible, we attempted to spot the frog visually. Alternatively, we triangulated the location as closely as possible. Consecutive movements longer than approximately 15 m were recorded by averaging 30 GPS readings. The estimated relative error between two GPS points was approximately 5–8 m. For smaller-scale movements that would not be well represented via GPS signal, we measured the distance and the direction from the previous location using a precision compass (Recta DP-10 or Suunto Tandem, Suunto, Vantaa, Finland) and a laser distance-meter (DLE 50, Robert Bosch GmbH, Gerlingen, Germany). All data were recorded using a handheld GIS/GPS device (MobileMapper 10; Spectra Precision, Westminster, CO, USA) with the GIS software ArcPAD 10 (ESRI, Redlands, CA, USA). Eight translocated frogs were recaptured and shortly handled one or two times to change the radio-transmitter or check the fit of the waistband. We attempted to track the frogs until they returned to the immediate vicinity of the capture point (i.e. home territory). The tracking of two individuals was terminated by a malfunction and loss of transmitter after 7 and 12 days, respectively. In addition, one frog had not moved from the release site after 7 days. We untagged and returned this individual back to its territory.

Data analysis
Visualization of trajectories and extraction of coordinates were done in the GIS software ArcGIS 10 (ESRI) (Dataset 1). We used the R statistical software (R Foundation for Statistical Computing, Vienna, Austria) package 'adehabitatLT' (https://cran.r-project.org/web/packages/adehabitatLT/vignettes/adehabitatLT.pdf) to calculate time, distance, speed and the absolute angle between successive points for each trajectory (Dataset 2). For comparing the frogs' movement speed we excluded the night-time, when this species does not move. We used Spearman's rank correlation to test whether the frogs' movement speed increased during the tracking period. For visualization, we plotted the distance remaining to the home territory as a function of time elapsed since the translocation. To test for initial homeward orientation after release, we compared the bearing between the release point and two points early in the movement trajectory to the correct homewards bearing. These two points were the closest positions available from the release site in 5–20 m and 20–50 m ranges. Individuals that did not have a recorded position within these distance ranges were excluded from the respective analysis. Significant homeward orientation was tested using Rayleigh's test for unimodal distribution of angles. Rayleigh's test was performed with the circular statistics program Oriana 4.02 (Kovach Computing Services, Pentraeth, Isle of Anglesey, UK). To further quantify the precision of orientation during homing, we calculated: (1) the path straightness coefficient, (2) the absolute angular deviation from homewards orientation and (3) linear deviation from the straight-line path (see Dataset 2 and Table S1). The straightness coefficient (SC) is defined as the ratio between the straight-line distance from release to the territory and the actual path distance (SC ranges from 0 to 1, with 1 indicating a perfectly straight trajectory). The angular deviation was calculated as the absolute angular difference between the ideal direction (angle from each tracking location to the territory) and the actual direction of the frog's movement (angle from each tracking location to the next one). The linear deviation was calculated as the distance from the straight-line path, i.e. the perpendicular deviation of each tracking location from the straight path. We used Spearman's rank correlation to test whether the translocation distance influenced homing precision measured as: (1) SC of the full homing trajectory,

(2) average angular deviation of the first 25% and the full trajectory and (3) average linear deviation of the first 25% and the full trajectory. To visualize the dynamics of homing precision during the entire trajectory, we grouped the frogs based on translocation distance: 200–300 m, 400–500 m and 700–800 m. We normalized the translocation distance to 100% for all frogs and plotted angular and linear deviation as a function of the percentage of homing completed. We plotted the smoothed averages and their respective standard errors for each group using a 50-m averaging bin and a sliding smoothing window of 10 data points. The plots were created in MATLAB 2017a (The MathWorks Inc., Natick, MA, USA).

Permits and ethical statement

The research was performed under the official research permit no. 007-2014-SERFOR-DGGSPFFS, given to Dr Juliane Diller by the Peruvian forestry and nature conservancy authority SERFOR (Servicio Forestal y de Fauna Silvestre). The experiments were conducted in strict accordance with the European and Peruvian law and following the 'Guidelines for use of live amphibians and reptiles in the field and laboratory research' by the Herpetological Animal Care and Use Committee (HACC) of the American Society of Ichthyologists and Herpetologists.

RESULTS AND DISCUSSION

Ten out of 12 translocated males returned to their home territory during our observation period (Table S1) and full homing trajectories were obtained for nine individuals. Frogs returned from all translocation distances. In general, males spent up to several days near the release sites (Fig. 1) and then returned via a direct path (Fig. 2). Only three individuals appeared disoriented (one from 400 m and two from 600 m) and did not move towards home (Fig. 2). Out of these three males, two did not return home during the tracking period and one lost the tag but was eventually recaptured at the home territory. The remaining nine frogs moved 0 to 13.9 m (mean=3 m, s.d.=4.4 m) farther away from home after the release, before moving homewards (Fig. 1). Homing males took between 1.8 and 11.0 days (mean=6.3 days, s.d.=2.9 days) to return.
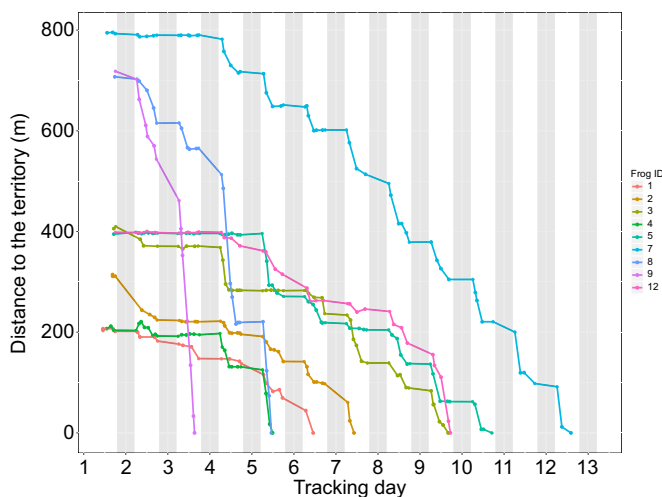

Fig. 1. Spatio-temporal pattern of homing in *Ameerega trivittata* translocated from 200 m to 800 m. The figure shows the remaining distance to territory over the course of tracking. The night periods are shaded in gray. Each line represents a different individual and each dot represents a tracking point. The far-left points represent the release after translocation (200–800 m). The far-right points of each line represent the respective arrival at the home territory (0 m). Frogs were translocated and tracked non-simultaneously.
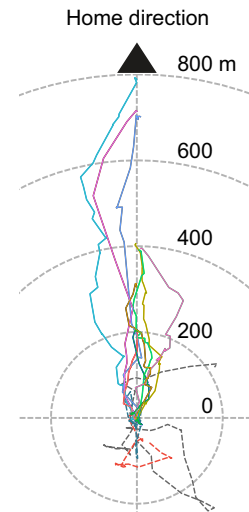

Fig. 2. Homing trajectories over 800 m of 12 male *A. trivittata* translocated from the territory. All trajectories are normalized to a common release site (center of the plot) and home direction (0 deg). Each line corresponds to a different individual. Trajectories of three disoriented individuals are marked with dashed lines.

Before homing, males spent between 0.7 and 3.6 days (mean=1.8 days, s.d.=1.2 days) within 20 m from the release site. The frogs' movement speed (excluding the nights) was on average 11.4 m h^{-1}, with a maximum of 64.2 m h^{-1}. The average speed per day increased significantly over the tracking period (Spearman's rank correlation: r_S=0.47, P<0.001; Fig. 2).

Frogs showed a trend towards homeward orientation at 5–20 m (expected bearing=0 deg, mean vector=300.5 deg, 95% CI=255–346 deg, Rayleigh test P=0.05, n=10) and a strong homewards orientation at 20–50 m (expected bearing=0 deg, mean vector=349 deg, 95% CI=317–22 deg, Rayleigh test P<0.003, n=7) from the release site. Frogs returned home with an average SC of 0.81 (s.d.=0.09), an average angular deviation of 48.11 deg (s.d.=16.59 deg) for the full trajectory and 58.31 deg (s.d.=21.5 deg) for the first 25% of the trajectory (Fig. 3A, Fig. S5A), and an average linear deviation from a straight line of 24 m (s.d.=13.30 m) for the full trajectory and 12.9 m (s.d.=8.5 m) for the first 25% of the trajectory (Fig. 3B, Fig. S5B). Linear deviation from the straight line was significantly higher for longer translocation distances (Spearman's rank correlation: $r_{Sfull\ trajectory}$=0.73, P=0.031; $r_{Sfirst\ 25\%\ of\ trajectory}$=0.72, P=0.037). Translocation distance did not have a significant effect on SC (Spearman's rank correlation: r_S=0.45, P=0.230) or angular deviation (Spearman's rank correlation: $r_{Sfull\ trajectory}$=0.02, P=0.982; $r_{Sfirst\ 25\%\ of\ trajectory}$=0.07, P=0.880).

The results suggest that frogs can use local cues in a map-like fashion to determine their position and the home direction from areas outside the range of their routine movements. The scale and the accuracy of homing in such a complex environment challenge our current understanding of mechanisms and the sensory basis of amphibian orientation. Beaconing, i.e. following cues originating from the goal, has been suggested as a potential orientation mechanism for several amphibians migrating to and away from large breeding ponds in temperate regions (Bee, 2007; Grubb, 1973; Joly and Miaud, 1993; Sinsch and Kirst, 2016). However, direct cues originating from the territory are very unlikely to be perceived over hundreds of meters in dense rainforest. Further and contrary to
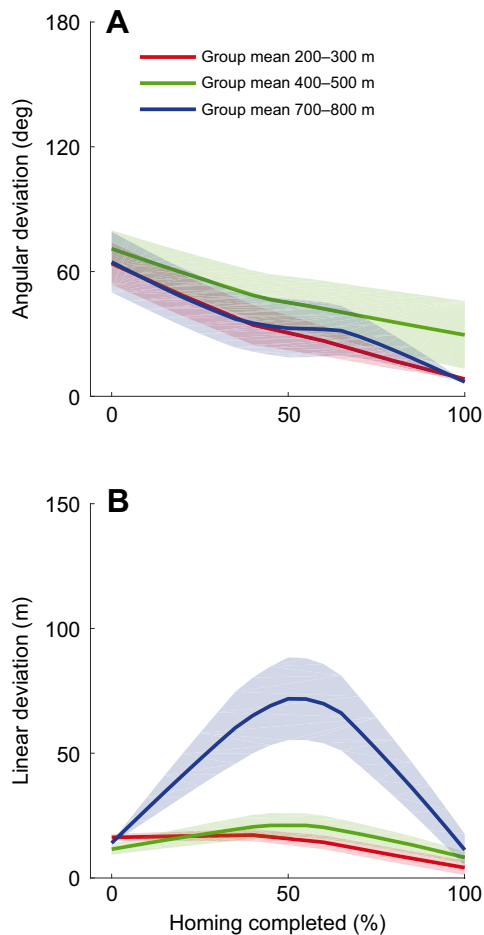
Fig. 3. Homing precision as a function of homing path completed. Each line represents a smoothed group mean of three frogs translocated to 200–300 m, 400–500 m or 700–800 m from their territory (total *n*=9), where 0% corresponds to the release site and 100% to the arrival at the home territory. The shading represents the respective standard error of each mean. The group mean and standard error were calculated using 50-m averaging bins and then normalized for the translocation distance for each frog (see Fig. S5 for non-normalized curves). Homing precision was measured as (A) absolute angular deviation from the ideal angle (i.e. home direction) and (B) linear deviation from a straight-line path from release site to home territory.

what would be predicted by beaconing, the accuracy of initial orientation was not strongly influenced by the translocation distance (Fig. 3B). Map-like navigational flexibility has been mostly studied in species moving in open spaces, such as in birds, bats and honeybees in flight, where large-scale visual, olfactory or magnetic gradients are available (Jacobs and Menzel, 2014; Tsoar et al., 2011; Wallraff, 2001). Distant visual landmarks are key in explaining navigational flexibility in insects homing from several hundred meters (Cheng, 2012; Pritchard and Healy, 2017), but the visibility in the forest understory is generally limited (Fig. S1). Olfactory gradients, such as proposed for bird navigation (Wallraff, 1980; Wiltschko and Wiltschko, 2009), seem unlikely because of limited airflow directionality in dense vegetation, but the odor movements in the forest and the olfactory capacity of frogs are poorly understood. Magnetic map sense has been implicated in the long-distance homing of several species (Lohmann et al., 2007), including one newt species (Fischer et al., 2001). Magnetic map sense is unlikely to account for the observed orientation precision over several hundred meters because of shallow global gradients of

the earth's magnetic field (Phillips, 1996). However, local magnetic anomalies could create steeper local gradients and the sensitivity limits of amphibian magnetoreception remain unknown.

Most tracked frogs choose the correct initial direction with very little exploration, but often after stationary periods lasting several days; a pattern already observed in another poison frog species (Pašukonis et al., 2014a,b). These long and variable waiting periods are probably influenced by several factors, such as intrinsic motivation and weather conditions, but they could also be indicative of orientation mechanisms. Olfactory, acoustic and magnetic landscapes show strong temporal variation. To use these cues for orientation, frogs may need to wait for favorable detection conditions or integrate the variation over time. Both acoustic and olfactory cues are abundant in complex habitats and anuran amphibians are known to rely heavily on both sensory domains for their reproductive behavior as well as orientation (e.g. Byrne and Keogh, 2007; Gerhardt and Huber, 2002; Grubb, 1973; Schulte et al., 2011). In addition, several amphibians, including toads and frogs, have been shown to use a magnetic compass mechanism (e.g. Diego-Rasilla et al., 2005; Landler and Gollmann, 2011; Shakhparonov and Ogurtsov, 2017), which might be particularly relevant in habitats with limited visibility.

Results of several translocation studies suggest that amphibians require familiarity with an area for homing (Oldham, 1967; Pašukonis et al., 2014a; Sinsch and Kirst, 2016). The extent of natural movements of most amphibians remains unknown and probably underestimated (Sinsch, 2014), but it seems that homing ability in some amphibians can be at least partially extrapolated outside these home ranges. For example, one sedentary newt species (*Taricha rivularis*) can return to natal creek sections after being translocated several kilometers (Twitty et al., 1964; Twitty et al., 1967). At a smaller scale, the homing success in the poison frog *A. femoralis* is highest up to 200 m, but some males return from up to 400 m (Pašukonis et al., 2013; Pašukonis et al., 2014a), which is double the maximum natural movement range ever observed in this species (Beck et al., 2017; Ringler et al., 2009; Ringler et al., 2013). Frogs of this species are disoriented when translocated to an unfamiliar nearby area across a river, suggesting that some experience with the local cues is necessary for navigation (Pašukonis et al., 2014a). However, the river could disrupt distant cues, such as odor and sound, required for extrapolation. Males of *A. trivittata* spend most of their time inside small territories approximately 5 to 15 m in diameter (Neu et al., 2016; Roithmair, 1994). They routinely shuttle tadpoles outside their territory to widely distributed aquatic sites (Luiz et al., 2015; Roithmair, 1994) and we have observed males transporting tadpoles up to 380 m from their territory (A.P. and M.-C.L., unpublished data). Despite this fact, the low movement capacity of these small terrestrial frogs (maximum speed of 64 m h^{-1}) and the fact that males spend most time inside their small territories make it very unlikely that the arbitrarily selected release sites were in the areas routinely visited by the frogs. Contrary to our expectation, males returned from the longest translocation distances (800 m), so the maximum homing distances for some individuals are likely to be even higher. Further, there was generally little decrease in the accuracy of initial orientation with increasing translocation distances. We consider it unlikely that frogs would have explored and learned detailed landmarks over this entire area (i.e. a perimeter of at least 800 m around the territory) and speculate that homing ability in poison frogs is dependent on some learned cues that can be extrapolated. Such a 'mosaic map' (Wallraff, 1980; Wiltschko and Wiltschko, 1978; Wiltschko and Wiltschko, 2009) with extended landmarks

that could be partially extrapolated has been proposed for short-distance homing in pigeons. We speculate that frogs can integrate learned acoustic, olfactory or magnetic landmarks with a compass mechanism into spatial representations that allow partial extrapolation to and navigation from places that had not been directly explored before.

Navigational performance revealed in this study challenges our current explanations for map-like behaviors in amphibians. Frogs can take direct routes to small out-of-sight goals from arbitrary locations outside their typical home ranges and in a habitat where distant landmarks are limited. While learning plays an important role in poison frog navigation, it is unlikely that frogs know and recognize landmarks at the immediate vicinity of the release site. More research on the spatio-cognitive and sensory abilities of tropical frogs and other animals from these environments is needed before we begin to understand how they navigate.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization, resources & funding acquisition: A.P., W.H.; Methodology & analysis: A.P., M.C.L.; Original draft: A.P.; Investigation, review & editing: A.P., M.C.L., W.H.

Supplementary information
Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.169714.supplemental

References

Beck, K. B., Loretto, M.-C., Ringler, M., Hödl, W. and Pašukonis, A. (2017). Relying on known or exploring for new? Movement patterns and reproductive resource use in a tadpole-transporting frog. *PeerJ* **5**, e3745.

Bee, M. A. (2007). Selective phonotaxis by male wood frogs (*Rana sylvatica*) to the sound of a chorus. *Behav. Ecol. Sociobiol.* **61**, 955-966.

Bogert, C. M. (1947). Results of the Archbold expeditions No. 57. A field study of homing in the Carolina toad. *Am. Mus. Novit.* **1355**, 1-24.

Byrne, P. G. and Keogh, J. S. (2007). Terrestrial toadlets use chemosignals to recognize conspecifics, locate mates and strategically adjust calling behaviour. *Anim. Behav.* **74**, 1155-1162.

Cheng, K. (2012). How to navigate without maps: the power of taxon-like navigation in ants. *Comp. Cogn. Behav. Rev.* **7**, 1-22.

Cheng, K. and Jeffery, K. (2017). Spatial cognition. In *APA Handbook of Comparative Psychology: Perception, Learning, Cognition* (ed. J. Call), pp. 463-483. Washington, DC: American Psychological Association.

Diego-Rasilla, F. J., Luengo, R. M. and Phillips, J. B. (2005). Magnetic compass mediates nocturnal homing by the alpine newt, *Triturus alpestris*. *Behav. Ecol. Sociobiol.* **58**, 361-365.

Dole, J. W. (1968). Homing in leopard frogs *Rana pipiens*. *Ecology* **49**, 386-399.

Ferguson, D. E. (1971). The sensory basis of orientation in amphibians. *Ann. N. Y. Acad. Sci.* **188**, 30-36.

Fischer, J. H., Freake, M. J., Borland, S. C. and Phillips, J. B. (2001). Evidence for the use of magnetic map information by an amphibian. *Anim. Behav.* **62**, 1-10.

Gerhardt, H. C. and Huber, F. (2002). *Acoustic Communication in Insects and Anurans: Common Problems and Diverse Solutions*. Chicago, IL: University of Chicago Press.

Grubb, J. C. (1973). Olfactory orientation in *Bufo woodhousei fowleri*, *Pseudacris clarki* and *Pseudacris streckeri*. *Anim. Behav.* **21**, 726-732.

Ishii, S., Kubokawa, K., Kikuchi, M. and Nishio, H. (1995). Orientation of the toad, *Bufo japonicus*, toward the breeding pond. *Zoolog. Sci.* **12**, 475-484.

Jacobs, L. F. and Menzel, R. (2014). Navigation outside of the box: what the lab can learn from the field and what the field can learn from the lab. *Mov. Ecol.* **2**, 3.

Jameson, D. L. (1957). Population structure and homing responses in the Pacific tree frog. *Copeia* **1957**, 221-228.

Joly, P. and Miaud, C. (1993). How does a newt find its pond – the role of chemical cues in migrating newts (*Triturus alpestris*). *Ethol. Ecol. Evol.* **5**, 447-455.

Landler, L. and Gollmann, G. (2011). Magnetic orientation of the common toad: establishing an arena approach for adult anurans. *Front. Zool.* **8**, 6.

Lohmann, K. J., Lohmann, C. M. F. and Putman, N. F. (2007). Magnetic maps in animals: nature's GPS. *J. Exp. Biol.* **210**, 3697-3705.

Luiz, L. F., Contrera, F. A. L. and Neckel-Oliveira, S. (2015). Diet and tadpole transportation in the poison dart frog *Ameerega trivittata* (Anura, Dendrobatidae). *Herpetol. J.* **25**, 187-190.

Mascanzoni, D. and Wallin, H. (1986). The harmonic radar: a new method of tracing insects in the field. *Ecol. Entomol.* **11**, 387-390.

Matthews, K. R. (2003). Response of mountain yellow-legged frogs, *Rana muscosa*, to short distance translocation. *J. Herpetol.* **37**, 621-626.

Neu, C. P., Bisanz, S. S., Nothacker, J. A., Mayer, M. and Lötters, S. (2016). Male and female home range behavior in the Neotropical poison frog *Ameerega trivittata* (Anura, Dendrobatidae) over two consecutive years. *South Am. J. Herpetol.* **11**, 212-219.

Nowakowski, A. J., Otero Jiménez, B., Allen, M., Diaz-Escobar, M. and Donnelly, M. A. (2013). Landscape resistance to movement of the poison frog, *Oophaga pumilio*, in the lowlands of northeastern Costa Rica. *Anim. Conserv.* **16**, 188-197.

Oldham, R. S. (1967). Orienting mechanisms of the green frog *Rana clamitans*. *Ecology* **48**, 477-491.

Papi, F. (1990). Homing phenomena: mechanisms and classifications. *Ethol. Ecol. Evol.* **2**, 3-10.

Pašukonis, A., Ringler, M., Brandl, H. B., Mangione, R., Ringler, E. and Hödl, W. (2013). The Homing frog: high homing performance in a territorial dendrobatid frog *Allobates femoralis* (Dendrobatidae). *Ethology* **119**, 762-768.

Pašukonis, A., Warrington, I., Ringler, M. and Hödl, W. (2014a). Poison frogs rely on experience to find the way home in the rainforest. *Biol. Lett.* **10**, 20140642.

Pašukonis, A., Loretto, M.-C., Landler, L., Ringler, M. and Hödl, W. (2014b). Homing trajectories and initial orientation in a Neotropical territorial frog, *Allobates femoralis* (Dendrobatidae). *Front. Zool.* **11**, 29.

Pašukonis, A., Trenkwalder, K., Ringler, M., Ringler, E., Mangione, R., Steininger, J., Warrington, I. and Hödl, W. (2016). The significance of spatial memory for water finding in a tadpole-transporting frog. *Anim. Behav.* **116**, 89-98.

Phillips, J. B. (1996). Magnetic navigation. *J. Theor. Biol.* **180**, 309-319.

Phillips, J. B., Adler, K. and Borland, S. C. (1995). True navigation by an amphibian. *Anim. Behav.* **50**, 855-858.

Pichler, C., Weinlein, S., Kopeinig, L. and Pašukonis, A. (2017). Homing performance in a territorial dendrobatid frog, *Allobates talamancae*. *Salamandra* **53**, 309-313.

Pritchard, D. J. and Healy, S. D. (2017). Homing and navigation. In *APA Handbook of Comparative Psychology: Perception, Learning, and Cognition* (ed. J. Call), pp. 485-508. Washington, DC: American Psychological Association.

Ringler, M., Ursprung, E. and Hödl, W. (2009). Site fidelity and patterns of short- and long-term movement in the brilliant-thighed poison frog *Allobates femoralis* (Aromobatidae). *Behav. Ecol. Sociobiol.* **63**, 1281-1293.

Ringler, E., Pašukonis, A., Hödl, W. and Ringler, M. (2013). Tadpole transport logistics in a Neotropical poison frog: indications for strategic planning and adaptive plasticity in anuran parental care. *Front. Zool.* **10**, 67.

Roithmair, M. E. (1994). Male territoriality and female mate selection in the dart-poison frog *Epipedobates trivittatus* (Dendrobatidae, Anura). *Copeia* **1994**, 107-115.

Shakhparonov, V. V. and Ogurtsov, S. V. (2017). Marsh frogs, *Pelophylax ridibundus*, determine migratory direction by magnetic field. *J. Comp. Physiol. A* **203**, 35-43.

Schulte, L. M., Yeager, J., Schulte, R., Veith, M., Werner, P., Beck, L. A. and Lötters, S. (2011). The smell of success: choice of larval rearing sites by means of chemical cues in a Peruvian poison frog. *Anim. Behav.* **81**, 1147-1154.

Sinsch, U. (1987). Orientation behaviour of toads (*Bufo bufo*) displaced from the breeding site. *J. Comp. Physiol. [A]* **161**, 715-727.

Sinsch, U. (1992). Amphibians. In *Animal Homing* (ed. F. Papi), pp. 213-233. Dordrecht: Springer.

Sinsch, U. (2006). Orientation and navigation in Amphibia. *Mar. Freshw. Behav. Physiol.* **39**, 65-71.

Sinsch, U. (2014). Movement ecology of amphibians: from individual migratory behaviour to spatially structured populations in heterogeneous landscapes. *Can. J. Zool.* **92**, 491-502.

Sinsch, U. and Kirst, C. (2016). Homeward orientation of displaced newts (*Triturus cristatus*, *Lissotriton vulgaris*) is restricted to the range of routine movements. *Ethol. Ecol. Evol.* **28**, 312-328.

Tsoar, A., Nathan, R., Bartan, Y., Vyssotski, A., Dell'Omo, G. and Ulanovsky, N. (2011). Large-scale navigational map in a mammal. *Proc. Natl. Acad. Sci.* **108**, E718-E724.

Twitty, V., Grant, D. and Anderson, O. (1964). Long distance homing in the newt *Taricha rivularis*. *Proc. Natl. Acad. Sci. U. S. Am.-Biol. Sci.* **51**, 51-58.

Twitty, V., Grant, D. and Anderson, O. (1967). Amphibian orientation: an unexpected observation. *Science* **155**, 352-353.

Wallraff, H. G. (1980). Olfaction and homing in pigeons: nerve-section experiments, critique, hypotheses. *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* **139**, 209-224.

Wallraff, H. G. (2001). Navigation by homing pigeons: updated perspective. *Ethol. Ecol. Evol.* **13**, 1-48.

Wells, K. D. (2007). *The Ecology & Behavior of Amphibians*. Chicago, IL: University of Chicago Press.

Weygoldt, P. (1987). Evolution of parental care in dart poison frogs (Amphibia: Anura: Dendrobatidae). *J. Zool. Syst. Evol. Res.* **25**, 51-67.

Wiltschko, W. and Wiltschko, R. (1978). A theoretical model for migratory orientation and homing in birds. *Oikos* **30**, 177-187.

Wiltschko, R. and Wiltschko, W. (2009). Avian navigation. *The Auk* **126**, 717-743.

Figure S1. Photographic panorama-view from one of the successful homing trajectory points showing the habitat structure. A) Photograph taken from higher-end perching height of a calling *A. trivittata* (approximately 1 m). B) Photograph taken from a usual perching height of a moving *A. trivittata* (approximately 0.3 m).
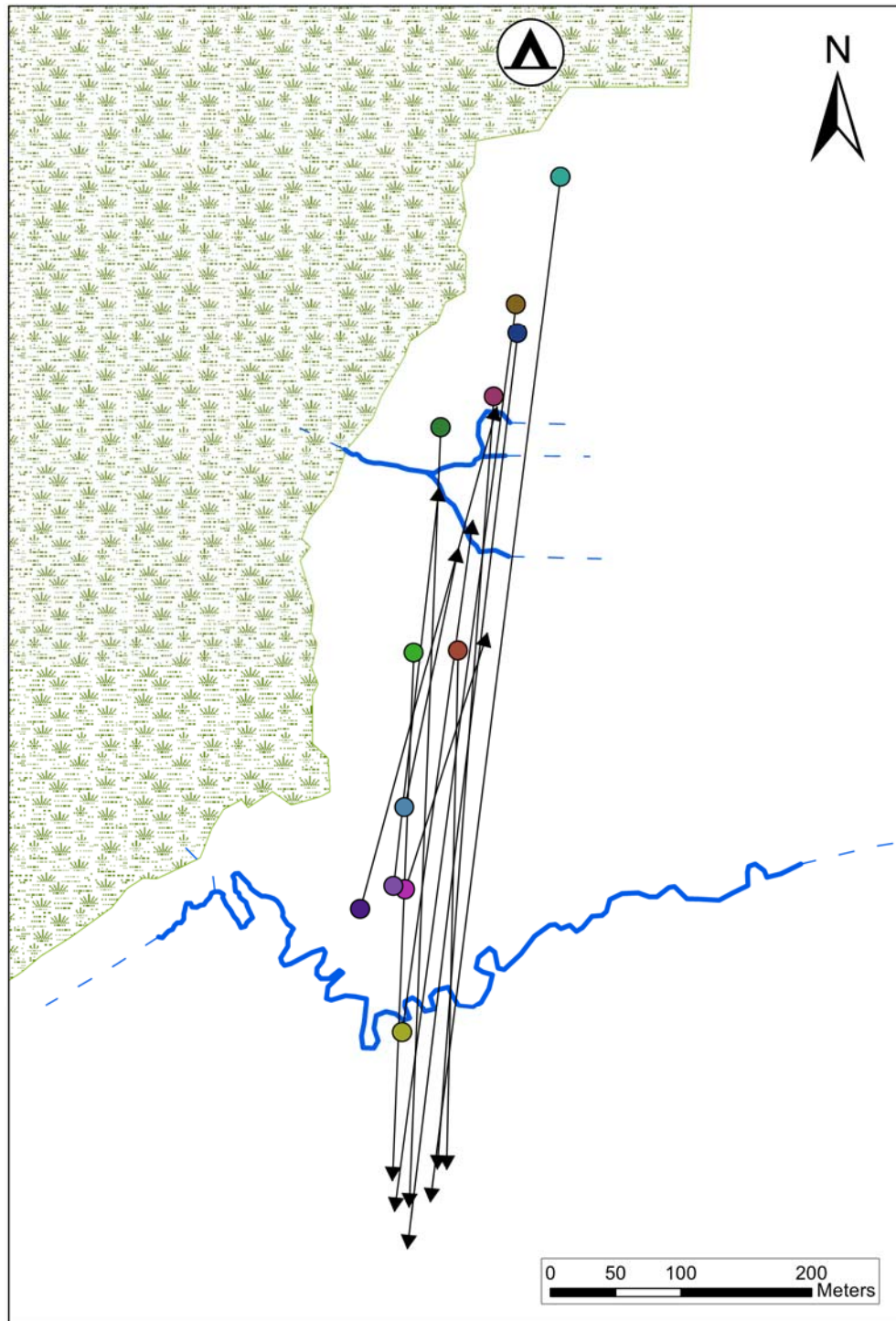
Figure S2. Map of the study area showing the territories (colored circles) and the release sites (arrowheads) of 12 translocated males. The area filled with "tussock" represents the pastureland bordering the study area. Blue lines represent the creeks. Camp symbol represents the field station.

Figure S3. Photograph of a male *A. trivittata* calling in his territory while wearing a miniature radio transmitter attached with a waistband made from fine silicone tubing.

Figure S4. Photograph of a male *A. trivittata* being placed in an airtight opaque container used for transporting frogs between the capture and the release site.
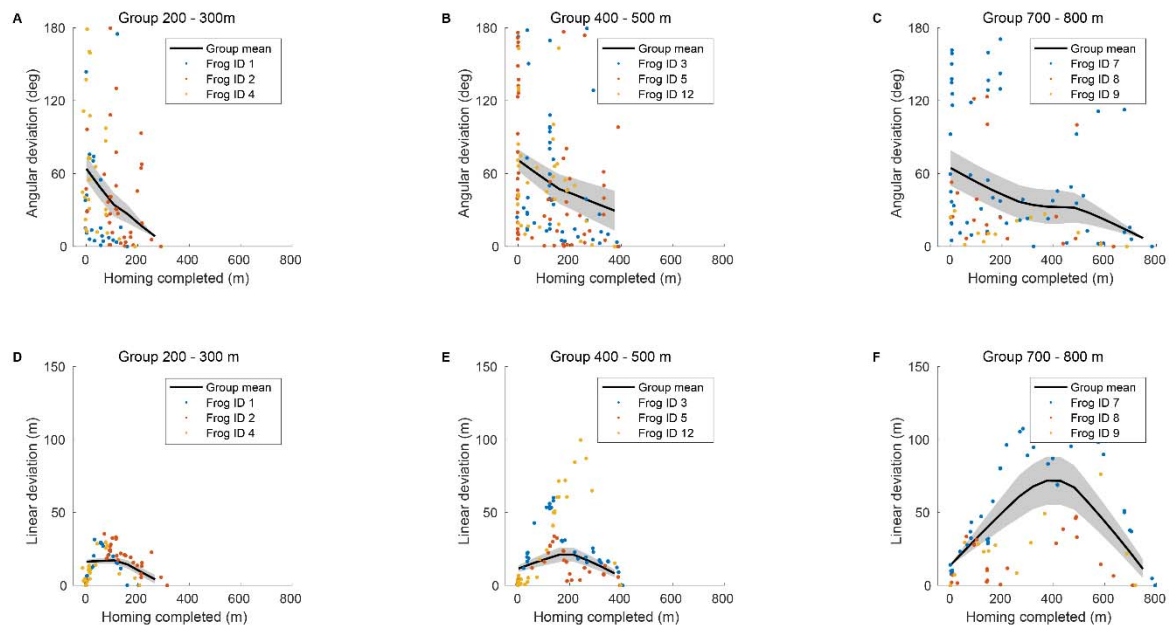
Figure S5. Homing precision as a function of homing path completed. Each plot shows three frogs homing from 200 – 300 m, 400 – 500 m, and 700 – 800 m back to their territory (total n = 9), where the far-left corresponds to the release site and far-right to the arrival at the home territory. Colored dots represent tracking points along the trajectory and each line represents a smoothed group mean. The shading represents the respective standard errors of each mean. The group mean and standard error were calculated using 50 m averaging bins and smoothed with a 10-point sliding window. The homing precision measured as A) B) C) absolute angular deviation from the ideal angle (i.e., home direction) and D) E) F) linear deviation from a straight-line path from the release site to the home territory.

Frog ID	Homing success	Transloc. dist. [m]	Homing dur. [h]	Mean speed [m/h]	Max. speed [m/h]	Linear deviation [m]	Abs. ang. deviation [deg]	SC	Orient. 5-20 m [deg]	Orient. 20-50 m [deg]
1 (Señor Estanque)	+	200	120.0	4.3	11.4	14.6	35.5	0.9	287.2	331.1
2 (Lianida)	+	300	137.8	5.5	31.7	19.5	40.0	0.8	311.8	NA
3 (Phoneutria)	+	400	190.9	6.0	32.1	31.3	54.8	0.8	172.2	28.4
4 (Mr. Bullet Ant)	+	200	94.8	7.6	30.1	11.7	67.7	0.6	221.3	19.3
5 (Ricky Martin)	+	400	215.8	4.4	38.3	9.0	55.8	0.8	70.3	NA
6 (Drunken Sailor)	-	600	NA	10.5	37.7	70.3	75.6	0.2	5.7	206.2
7 (Herr Humboldt)	+	800	264.8	8.8	38.1	52.1	63.3	0.8	297.6	327.9
8 (La Tigresa)	+	700	89.4	19.4	55.4	18.8	46.5	0.9	336.0	3.2
9 (Speedy Gonzales)	+	700	45.2	39.9	64.2	30.3	13.5	0.9	335.6	NA
10 (Mick Jagger)	+[*]	400	NA	6.5	40.5	NA	NA	NA	318.2	281.2
11 (Adam)	-	600	NA	8.7	39.6	12.0	57.7	0.2	151.0	NA
12 (Delfin)	+	400	191.2	6.4	23.5	28.6	55.9	0.7	277.4	3.2

Table S1: Summary table of all measured variables for each translocated frog: homing success ("+" stands for successful homing), translocation distance, homing duration, mean and maximum speed, mean linear deviation from straight line trajectory to home, mean absolute angular deviation from homeward orientation, straightness coefficient, initial orientation bearings within 5 – 20 m and 20 – 50 m from the release site.
* Transmitter malfunction. Frog recaptured home but full trajectory not available.

Dataset 1

Click here to Download Dataset 1

Dataset 2

Click here to Download Dataset 2