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TESIS PARA OPTAR POR EL GRADO DE LICENCIATURA EN BIOLOGÍA CON

ÉNFASIS EN ZOOLOGÍA

Trayectorias y comportamiento de "homing"

de la rana venenosa *Oophaga pumilio*:

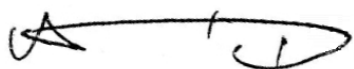El rol de pistas visuales durante la navegación

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DEDICATORIA

A toda mi familia que siempre ha sido un apoyo incondicional, por ser ejemplo de

constancia y dedicación.

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escucharme y ayudarme cuando lo he necesitado.

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RESUMEN

Las ranas venenosas neotropicales (Dendrobatidae) muestran comportamientos espaciales complejos que incluyen rangos de hogar permanentes, defensa territorial, transporte de renacuajos y en algunas especies, visitas posteriores de hembras para alimentar a los renacuajos con huevos infértiles. Las habilidades de navegación de los dendrobátidos son excepcionales, son capaces de orientarse en línea recta desde largas distancias. Algunas especies se desempeñan mejor cuando navegan en sitios familiares. Experimentos de laboratorio han demostrado que algunas ranas venenosas pueden usar señales visuales para localizar objetivos. Sin embargo, la naturaleza de la información visual que utilizan estas ranas en entornos naturales aún no está clara. Por ejemplo, la rana venenosa *Oophaga pumilio*, es capaz de regresar a su territorio hasta desde 30m en ambientes visualmente complejos. Sin embargo, se sabe poco sobre los mecanismos subyacentes a esta habilidad. Aquí, caractericé el comportamiento de homing y las trayectorias de machos *Oophaga pumilio* y evalué el papel de las posibles pistas visuales que podrían guiar la navegación espacial en entornos naturales. Desplacé a 28 machos territoriales a 8m de sus territorios y los coloqué en un goniómetro para visualizar los ángulos de salida. Medí la latencia para salir del goniómetro, la orientación inicial y el tiempo total de regreso al territorio. También medí las características de sinuosidad y orientación de las trayectorias de las ranas. Comparé el comportamiento de homing entre áreas abiertas y el bosque y evalué el papel de la información visual en el desempeño de homing. La complejidad visual fue mayor en el bosque que en áreas abiertas. El bosque tuvo valores más bajos sky ratio e información rotacional. En áreas abiertas todas las ranas regresaron a su territorio en 3 horas, mientras que en el bosque el 35% de los individuos no regresaron a su territorio. Solo las ranas de áreas abiertas se orientaron al territorio al salir del goniómetro. La latencia para salir del goniómetro aumentó conforme la disminución de la información rotacional. Además, esta latencia predijo el éxito de homing, ya que las ranas que tardaron más en salir del goniómetro eran menos propensas a regresar al territorio con éxito. Las trayectorias fueron similares entre sitios y no se vieron afectadas por las diferencias en la información visual disponible en el sitio de liberación. Los machos viajaron en casi en línea recta y generalmente se orientaron a lo largo de la trayectoria. Sin embargo, los machos en el bosque se movieron más lento que los machos en áreas abiertas. Estos resultados añaden evidencia a la noción general de que *O. pumilio*, como otros dendrobátidos, tiene una gran capacidad de navegación. Además, mostré un papel importante de las señales visuales mediante la información rotacional en la determinación de la orientación inicial del territorio. Juntos, estos resultados sugieren que la información visual podría desempeñar un papel importante durante la navegación. Sin embargo, se necesitan más estudios de campo para entender cómo la información visual se integra con otras señales y cómo esto podría afectar el rendimiento de la navegación en los anuros.

Palabras clave
Complejidad visual, comportamiento espacial, cuido parental, Dendrobatidae, navegación animal.

ABSTRACT

Neotropical poison frogs (Dendrobatidae) show complex spatial behaviors which include permanent home ranges, territorial defense, tadpole transport, and, in some species, subsequent visits by females to feed tadpoles with unfertilized eggs. The navigational abilities of dendrobatids are exceptional, as they are capable of homing in a straight-line from long distances. Some species perform better when navigating in familiar sites. Laboratory experiments have shown that some poison frogs can use visual cues to locate targets. However, the nature of the visual information being used by these frogs under natural settings remains unclear. For example, it is well known that the strawberry poison frog, *Oophaga pumilio,* is capable of successful homing from up to 30m in visually-complex. However, little is known about the mechanisms underlying this ability. Here, we characterized the homing behavior and trajectories of male *Oophaga pumilio,* and evaluated the role of possible visual cues that could guide spatial navigation under natural settings. We displaced 28 territorial males 8 meters away from their territories and placed them on a goniometer to visualize exit angles. We measured latency to exit the goniometer, initial orientation, and total time for successful homing. We also measured the sinuosity and orientation characteristics of the frogs' trajectories. We compared homing behavior between open areas and the forest and evaluated the role of visual information in homing performance. Visual complexity was higher in the forest than in open areas. The forest had lower values of sky ratio and rotational information. All frogs homed successfully within 3 hours in open areas, whereas 35% of displaced individuals in forests did not home successfully. Only frogs from open areas were territory-oriented when exiting the goniometer. The latency to exit the goniometer increased when less rotational information was available. Furthermore, this latency predicted homing success, as frogs that took more time exiting the goniometer were less prone to home successfully. Homing trajectories were similar between sites and were not affected by differences in visual information available at the release site. Males traveled in almost straight lines and were usually oriented along the trajectory. However, males in the forest moved more slowly than males in open areas. Our results add evidence to the general notion that *O. pumilio,* like other dendrobatids, has a strong navigational ability. Furthermore, we show an important role of visual cues via rotational information in determining initial orientation towards the territory. Together these results suggest that visual information could play an important role during navigation. However, more field studies are needed to unravel how visual information is integrated with other cues and how this could affect navigation performance in anurans.

Keywords
Animal navigation, Dendrobatidae, parental care, spatial behavior, visual complexity.

INTRODUCTION

Movements and migrations are an essential part of the life history of most animals (Papi 1990). Because of their phylogenetic position, studying navigational mechanisms in anurans may help to unravel the evolution of spatial cognition in vertebrates (Liu et al. 2019). Less than a decade ago, knowledge about anuran navigation was limited to studies in the families Ranidae, Hylidae, and Bufonidae (e.g. Taylor & Ferguson 1970, Grubb 1976, Adler 1980, Sinsch 1992, Christie et al. 2010, Buxton et al. 2015, Daneri et al. 2015). These families are composed mainly of nocturnal and temperate species, which exhibit annual long-distance migrations at night (Pichler et al. 2017). This taxonomic limitation complicates the generalization of navigational mechanisms to clades that face different navigational challenges, such as the Neotropical poison frogs (Dendrobatidae), which rely on short but frequent daily movements, mainly during daylight hours (Grant et al. 2017).

The family Dendrobatidae includes 198 poison frog species that display a high diversity of spatial and parental care behaviors (Guillory et al. 2019). In general, individuals defend a territory within a home range (Grant et al. 2017, Vitt & Caldwell 2014). Parental care roles include guarding the egg clutch, transport of the tadpoles on the back into small water bodies in the forest, and, in a few species, females return to feed tadpoles with unfertilized eggs until metamorphosis (Donnelly 1989, Savage 2002, Wells 2007, Stynoski 2009, Ringler et al. 2013, Munteanu et al. 2016, Pichler et al. 2017). Tadpole deposition and feeding require that an individual navigates in and out of its territory multiple times to visit the same places. These spatial tasks and the underlying mechanisms of dendrobatid navigation are likely to differ dramatically from those of nocturnal, temperate anuran clades.

Recent studies with the species *Allobates femoralis, A. talamancae,* and *Ameerega tivittata* suggest that dendrobatids have sophisticated navigation abilities, as they are capable of successful homing after experimental displacements at distances of 20 to 900 m (Pašukonis et al. 2014a, Pichler et al. 2017, Nothacker et al. 2018). They show strong orientation when homing and travel straight to their home ranges (Pašukonis et al. 2014, Pašukonis et al. 2018). The extraordinary navigation abilities of dendrobatids suggest that they rely on experience with local cues to navigate (Ringler et al. 2013, Pašukonis et al. 2014a, Pašukonis et al. 2014b, Pašukonis et al. 2016, Liu et al. 2016, Pichler et al. 2017, Pašukonis et al. 2018, Liu et al. 2019). Previous studies have also led to the hypothesis that they use landmarks and

reconstruct so-called "cognitive maps" of their environment (Pašukonis et al. 2014b, Munteanu et al., 2016; Pašukonis et al., 2018, Liu et al. 2019).

Laboratory experiments have shown that dendrobatids can learn to locate targets using visual cues. For example, the Palm Rocket frog, *Rheobates palmatus,* learned to locate a refuge while guided by surrounding visual marks (Lüddecke 2003). Additionally, the Green-and-Black poison frog, *Dendrobates auratus,* used visual landmarks to solve a maze to find a shelter (Liu et al. 2016). *D. auratus* could also use the overall visual configuration to learn the position of an immersed platform (Liu et al. 2019). These studies suggest that dendrobatids may use visual information when navigating. However, little is known about the nature of the visual information being used by these frogs under natural settings. The use of visual information for navigation in natural settings has only been tested in toads using invasive methods that interrupt normal behavior such as blocking the optic nerve or covering the eyes (Sinsch 1987, 1988, 1992). Alternatively, quantifying the visual information is a noninvasive approach that could allow us to determine the role of visual information during navigation (Zeil et al. 2003). The use of visual information in navigation is well studied in insects (see Wystrach & Graham 2012), and we can utilize similar methodologies to improve our understanding of anuran navigation.

The dendrobatid species for which homing behavior and trajectories have been characterized inhabit only forested areas, and tadpole transport is performed exclusively by males, which travel long distances (up to 30 m in *A. femoralis*) and deposit several tadpoles at once (Pašukonis et al. 2014, Neu et al. 2016, Pichler et al. 2017, Pašukonis et al. 2018). Species differences in life history and ecology are likely to be reflected in navigation abilities, and, accordingly, homing distances appear to vary among dendrobatid species (Pichler et al. 2017, Pašukonis ABS meeting, 2020). The strawberry poison frog, *Oophaga pumilio*, inhabits forests as well as open areas adjacent to the forest. In this species, both females and males hold territories, females have larger home ranges than males, males guard fertilized egg clutches until hatching occurs, and females carry the tadpoles one-by-one on their backs to temporal water sources where they intermittently feed them with unfertilized eggs for six weeks (Donnelly 1989, Savage 2002, Meuche et al. 2011). Previous displacements studies have shown that *O. pumilio* is capable of homed from distances up to 30 m, however, the homing success decreases with distance (McVey et al. 1981, Nowakowski et al. 2013).

Furthermore, initial orientation is territory-directed at distances of 6, 12, and 25 meters (McVey et al. 1981, Nowakowski et al. 2013). The homing trajectories have not been characterized and would allow us to elucidate if the navigation abilities of this species resemble the ones of other dendrobatids. Expanding the study of navigation to species with different life histories is crucial for a better understanding of how the evolution of parental care roles influences navigation abilities and mechanisms.

In this study, we performed experimental displacements to quantify the homing trajectories and behavior of the strawberry poison frog, *O. pumilio*. Males of this species defend territories in the understory of tropical rainforest and open areas adjacent to the forest, such as pastures with sparse trees or bushes and forest gaps. We compared the homing characteristics of males in open areas and the forest. To test the role of visual cues during navigation, we used two parameters to quantify the visual information at the release site. We also performed another experiment to evaluate whether particular visual cues (i.e., from the canopy or the horizon) are more important during initial orientation towards the territory.

METHODS

Study site and species

We carried out fieldwork from August 2019 to August 2020, at La Selva Biological Station, Sarapiquí, in the northeastern region of Costa Rica (84°02' W10°26'N). The strawberry poison frog, *Oophaga pumilio*, is a small leaf-litter dwelling anuran commonly found in lowland moist and wet forests and surrounding cleared areas that range from eastern Nicaragua to northwestern Panama (Savage 2002). For experiments, we only considered males holding a territory, so that they would be motivated to navigate back to their territory, as has been demonstrated in homing experiments with this and other dendrobatid species (Pašukonis et al. 2013, Pašukonis et al. 2014a, Pichler et al. 2017). The territories of males (0.24 to 4.78 m^2 in size) usually include access to trees and water pools in the vegetation necessary for keeping the eggs moist and for depositing tadpoles (Donnelly 1989). At La Selva, males usually move in and out of their territory within a larger home range (2.26 to 15.07 m^2) (Donnelly 1989).

Localization of territory-holding males

   We used a playback technique to simulate an intruder to identify males that were holding a territory (Donnelly 1989). We located a calling male, placed a speaker (Photive, CYREN2, and Power: 5W) 1 m away from it, and played back the advertisement call of another male. For playbacks, we used a single advertisement call that was recorded at La Selva. Males usually respond to such simulated intrusions with visual and acoustic displays and by approaching the sound source (Donnelly 1989). If the male responded accordingly and approached the speaker, we caught it with an aquarium fishing net. To avoid resampling males in experiments, we took dorsal and ventral pictures with a digital camera following capture. Then, we transferred the frog to a sealed opaque container that we placed inside the frog's territory (i.e., on the ground, adjacent to the calling perch). We identified each territory with a unique code that was written on flagging tape tied to the surrounding vegetation.

Homing trajectories

   We performed experimental displacements in open areas and the forest (Fig. 1A, B). We displaced each male (still inside the opaque container) 8 m away from its territory in a randomized direction (either N, S, E, or W). Preliminary studies showed high homing success at this distance (SGM and FGS, unpublished data). Each male spent around 15 min in the container. We then, placed the frog in the center of a wooden goniometer board (1m in diameter) that contained angle marks every 22° (16 sectors in total), randomizing the sector of the goniometer that was pointing to the territory in each trial. To allow each frog to acclimate before starting a trial, we placed it in the center of the goniometer and immediately covered it with an opaque plastic funnel (diameter: 11cm, height: 10cm) (Fig. 1A, C). We then marked adjacent 1x1m^2 plots on the ground, starting at the center of the goniometer and extending towards the perch where the frog was calling from before capture. To mark the vertices of these quadrants, we used thin metal rods (350 mm and 2 mm thick) with a small piece of flagging tape surrounding the top. The total area covered by the plots was 48 m^2: 8 m long (the displacement distance) by 6 m wide (3 m to each side of the release site, centered at the goniometer). Assembly of the plot took around 20 min, which was ample time for frog acclimation under the funnel.

Figure 1. Experimental set-up for homing trials with territorial male *O. pumilio* at La Selva Biological Station after 8 m displacements in sites with distinct visual complexity. **A.** Assembled plot (8x6 m^2) in an open area with lower visual complexity. The picture was taken at the release site, pointing towards the frog's territory around the tree on the right. **B.** Part of an assembled plot in the forest, with higher visual complexity. **C.** Frog released at the middle of goniometer.

To begin the experiment, we lifted the funnel that was covering the frog with a single upward thrust by pulling, from outside the arena, a 1.5 m-long cord attached to the funnel throughout a hollow tube held horizontally above the goniometer. We used the plot on the ground as a template to draw the path taken by the frog in a smaller-scaled paper plot (graph paper with 2x2 cm squares). We also recorded each frog's initial orientation (the sector by which the frog exited the goniometer), the latency (time to exit the goniometer), and the total time required for successful homing. We followed the frog from 2 m away to avoid altering its homing behavior; accuracy was lost when attempting to follow frogs from longer distances. Because we did not know the exact size or shape of the territories, we defined a successful homing event as 75% progression along the total length of the displacement route (arrival within 1.5 m of) original calling perch). The maximum duration given to each frog to complete the homing task was three hours; after that time, the trial was considered an unsuccessful homing event. To eliminate possible chemical cues left by frogs tested previously, we cleaned the goniometer between trials, first with 70% ethanol, and then with tap water.

Effect of visual information on homing characteristics

To evaluate whether the visual information affects the homing performance of male *O. pumilio*, we calculated two parameters – rotational information and sky ratio – to describe the visual information available at the release site (8 m away from the territory), following the methodology seen in Wystrach et al. (2012). We took a 360° photo with a digital camera

(LG 360 CAM) at the goniometer center after each trial. We calculated the amount of rotational information available to the frog at the release site, defined as the average similarity between images separated by a rotation of 1 degree along the entire 360°. Higher values of rotational information indicate that the visual scenery differs strongly across viewing directions, allowing easier and more precise recovery of direction based on visual information. Lower values suggest that the visual landscape is similar across directions, making it harder to extract visual information that characterizes the direction of the territory. Sky ratio is an index of the amount of light (sky) vs. dark (terrestrial) pixels in the 360° visual field. Higher values indicate that the site has less vegetation and is thus exposed to more light coming from the sky.

We extracted the variables from each picture using Matlab (version R2020a). We transformed the 360 pictures into RAW format and resized the picture at 360 pixels. We then transformed the pictures into grayscale using the Blue layer and binarized it (black/white) using classical thresholding (Wystrach et al. 2012). Finally, we extracted the rotational information and sky radio indexes from the binary blue layer (for further details see Wystrach et al. 2012).

Effect of the canopy- and horizon-based visual information on the initial orientation
In a second experiment, we repeated the capture and displacement procedure described above, but with new male frogs that experienced four different conditions in a randomized order at the release site. The four conditions were: covered canopy (blocked visual cues from the canopy), covered horizon (blocked panoramic cues), covered canopy and horizon (no visual cues available), and control (no blocking of visual cues).

To block visual cues at the release site, we used double-layered, dark grey pieces of cloth. For the covered canopy condition, we hung a square piece of cloth (2.90 m^2) at 1 m height, centered above the goniometer, so that it shaded the goniometer and extended approximately one meter around it (Fig. 2A). For the covered horizon condition, we placed the cloth around the goniometer, forming a circular enclosure 1.5 m in diameter and 1 in height (Fig. 2B). For the covered canopy and horizon condition, we placed both covers around the goniometer (Fig. 2C). The control condition did not include any covers (Fig. 2D). The frogs spent approximately 12 minutes inside the opaque funnel at the center of the goniometer before starting the trial, which was less time than the first experiment because

we did not need to assemble plots. The experiment started when we lifted the funnel that was covering the frog. We recorded the initial orientation (the sector at which the frog exited the goniometer) and the latency to exit the goniometer. The trial finished when the frog exited the goniometer. After this, we placed the frog inside the opaque container and cleaned the goniometer with 70% ethanol and water. Each frog completed four trials in total (the four conditions), and trials were separated by approximately 20 minutes.

We chose a repeated-measures design for this experiment to control for variation in visual information among release sites. We only ran these experiments in open areas. We obtained the rotational information and sky ratio measurements at each release site, following the same procedure used in the homing experiment.

Figure 2. Set-up used in experiment 2. We manipulated the availability of visual cues during the initial orientation of displaced male *O. pumilio* at La Selva Biological Station using four conditions. A. Covered canopy (only cues from the horizon available). **B.** Covered horizon (only cues from the canopy available). **C.** Both canopy and horizon covered (no visual information available). **D.** Control (visual information available from the canopy and the horizon). A camera was placed at the center of the goniometer to take 360° data on visual information at each release site.

Data processing
Homing trajectories and effect of visual information on homing characteristics

We scanned the homing trajectories drawn on graph paper, digitized them, and transformed them into x, y coordinates using the software WebPlotDigitizer (version 4.2,

Copyright 2010-2019 Ankit Rohatgi). We standardized the digitization method in the following manner. To keep a constant number of points extracted from each route, we located each point at approximately every centimeter (in a straight line), which corresponded to 50 cm of the homing trajectory. We extracted three variables from the digitized trajectories: sinuosity indexes called straightness and meander (both ranging from 0 to 1) and path length. Path length corresponds to the total distance traveled in meters. To calculate both sinuosity indexes we divided the trajectory into segments of 0.3 meters. The meander index measures the average magnitude of directional changes between consecutive segments (see Schwarz et al. 2011). Higher meander values indicate that the trajectory often shows turns, that is, it meanders on the local scale. The straightness index measures whether or not all path segments - independently of their temporal sequence - are oriented in the same direction (values close to 1 indicate straight orientation) or different directions (values close to 0 indicate random trajectories). In other words, while 'meander' indicates sinuosity at the local scale, 'straightness' indicates whether the trajectory is consistent in its direction on the global scale. We extracted the variables using Matlab.

Statistical analysis
Homing trajectories and the role of visual cues on homing characteristics
　　For the first experiment, we first tested whether the initial orientation of the frog (in the first 50 cm) was territory-oriented (mu=0°) using a V test (circular, R package, Agostinelli & Lund 2017). Then, we tested for a difference in our parameters of available visual information (rotational information and sky ratio) between the forest and open areas using a Welch's t-test. We also compared the homing trajectory characteristics (meander, path length, and straightness) between forest and open areas using Welch´s t-tests. Finally, we performed linear models to assess whether the rotational information or the sky ratio predicted the meander and straightness indexes or path length.

　　We then compared the homing performance characteristics of successful males (those that completed the task within three hours) between the forest and open areas. We extracted from the initial orientation the variable 'angular error', which is the angle between the direction taken by the frog and the actual territory direction (a value ranging between 0 and 180 degrees), as viewed from the release site. To calculate the angular error for each frog, we first subtracted 180 from the actual initial orientation angle (at which the frog exited the

goniometer), then we calculated the absolute value and subtracted 180 from that value, taking absolute values a second time for the final value. We used Welch´s t-tests to compare the latency to exit the goniometer, the angular error, and the total time required for successful homing. We performed linear models to estimate whether visual information parameters (sky ratio and rotational information) predicted the angular error. We also performed generalized linear models (negative binomial error distribution) to estimate whether visual information parameters predicted the latency to exit the goniometer and the total time for successful homing.

Lastly, we tested whether the latency to exit the goniometer and the angular error differed between successful and unsuccessful males using a Welch's t-test. We performed logistic regressions (glm with binomial error distribution) to test whether the rotational information and the sky ratio predicted homing success. We also performed a logistic regression to test if the latency to exit the goniometer predicted homing success. To select the best model among the glm's, we used the Akaike information criterion with a correction for small sample sizes (AICc) to compare models, including a null model.

Effect of the canopy- and horizon-based visual information on the initial orientation

To determine whether visual information from the canopy or the horizon was most relevant, or if frogs required both types of cues for adequate orientation, we used a V test (mu=0) to test whether the initial orientation of each of the four conditions (covered canopy, covered horizon, canopy, and horizon covered, and control) was territory oriented. We used linear models to compare the angular error of the frog's initial orientation and the latency among treatments.

RESULTS

Homing trajectories and effect of visual information on homing characteristics
In the first experiment, we displaced 32 male *O. pumilio* in total. Four males (three from the forest and one from an open area) were excluded from this total because we lost their trajectory during the experiment**.** The frog from the open area disappeared after seeking shelter below a leaf; when we checked this leaf after 35 minutes, the frog was not there. Among the males of the forest, two of them we lost when they were confused with another frog that appeared in the arena. The next day, all 3 of these frogs had returned to their

territories. The fourth male was excluded because t it started calling near to the release site in what appeared to be the territory of another male, and both males engaged in a fight that involved calling and physical contact. Presumably, the target male lost the fight, and we did not check whether it returned to its original territory afterward. We ran all analyses with the remaining 28 valid trials (males we successfully tracked for 3 hours). Of those 28 frogs, 17 were from open areas and 11 from the forest. Overall, males showed high homing success within 3 hours (24 frogs, 85%); however, success differed between open areas (17 frogs, 100%) and forest (7 frogs, 64%) (Fisher's Exact test, p = 0.02). Among the four males that did not home successfully within the 3 hours, three of them were found in their territory on the next morning after the displacement. We placed the fourth male immediately back into its territory after the 3 hours (it had wandered 28 m in straight-line and in the complete opposite direction to its territory), so we do not know whether this male would have eventually homed back on its own like the others.

We compared the homing characteristics of successful males from open areas and the forest. The initial orientation of males in open areas was territory-directed on average (Z=0.42, p<0.01, Fig. 3A), while in the forest the initial orientation of males was randomly oriented (Z=0.29, p=0.07, Fig. 3B). However, we found that neither the angular error (mean±sd=57.54±44.92, t=0.33, df=7.12, p=0.75) nor the latency to exit the goniometer (57.74±56.00, t=1.25, df=6.49, p=0.25) were different between habitat types. The total time for successful homing was higher for individuals in the forest (forest: 115±63 vs. open: 15±16; t=3.20, df=6.50, p=0.02).
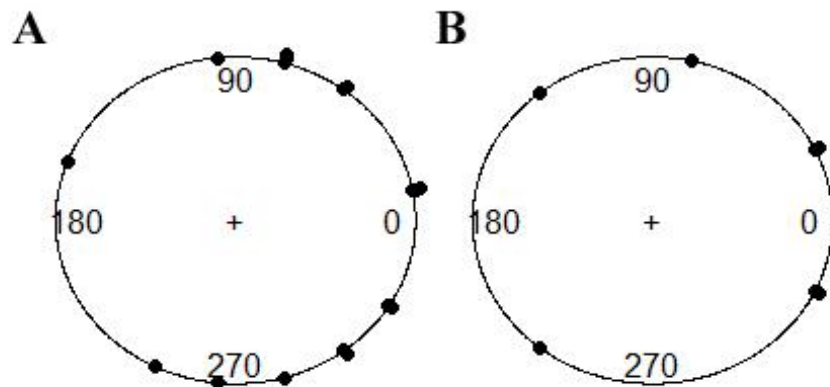
Figure 3. Initial orientation of male *O. pumilio* that homed successfully after being displaced 8 m away from their territories in **A**. Open areas (n=17) **B.** The forest (n=7). Overlapping dots are stacked one on top of another.

The available visual information for navigation differed between open areas and the forest. Open areas had higher values of rotational information (t=-4.30, df=22.39, p<0.001, Fig. 4A) and higher values of sky ratio (t=-3.70, df=25.815, p<0.01, Fig. 4B). We analyzed whether the rotational or sky ratio information or the site type (forest vs. open areas) predicted the latency to exit the goniometer, the angular error of the initial orientation, or the total time required for successful homing. We found that higher values of rotational information predicted faster exits from the goniometer (Table 1, Fig. 5, estimate < 0.0001, z=-2.43, p=0.01). The total time required for successful homing was best predicted by the site type, as frogs in the forest took longer to home (Table 1, estimate=-1.64, z=-4.15, p<0.001). When analyzing the angular error, we found that none of the models performed better than the null model (Table 1), suggesting that neither site type nor the two types of visual information were good predictors of angular error in this experiment.
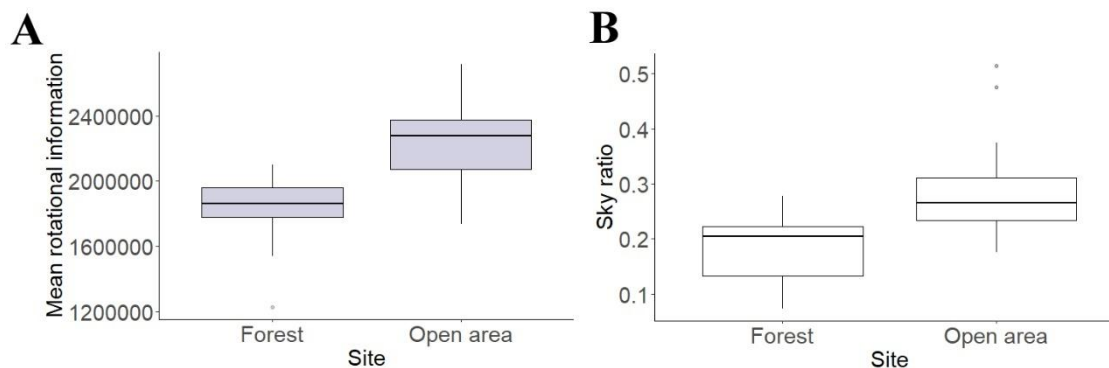
Figure 4. Comparison of the visual information available at the release sites, where male *O. pumilio* were displaced in homing experiments performed in the forest (n=17) and open areas (n=11). **A.** Rotational information. **B.** Sky ratio.

Table 1. Model selection of the different models considered for explaining the homing performance of successful male *O. pumilio* displaced 8m away from their territories. In bold, the chosen model(s) according to the Akaike Information criteria corrected for small sample sizes (AICc). **(**)** when the model showed significant results in any of the predictor variables

Response variable (Distribution)	Predictors	AICc
Angular error (gaussian)	Sky ratio + Site + Rotational information	250.65
	Sky ratio + Rotational information	247.65
	Sky ratio	244.91
	Rotational information	246.18
	Sky ratio * Rotational information	250.67
	Site * Rotational information	252.37
	Sky ratio * Site	248.94

	Site	246.38
	Null	243.87
Latency (negative binomial)	Sky ratio + Site + Rotational information	246.88
	Sky ratio + Rotational information	244.06
	Sky ratio	248.48
	Rotational information	**241.26** (**)
	Sky ratio * Rotational information	244.59
	Site * Rotational information	245.45
	Sky ratio * Site	244.02
	Site	244.46
	Null	246.25
Total time (negative binomial)	Sky ratio + Site + Rotational information	412.52
	Sky ratio + Rotational information	417.05
	Sky ratio	417.39
	Rotational information	415.77
	Sky ratio * Rotational information	420.27
	Site * Rotational information	412.29
	Sky ratio * Site	412.52
	Site	**406.43** (**)
	Null	418.91
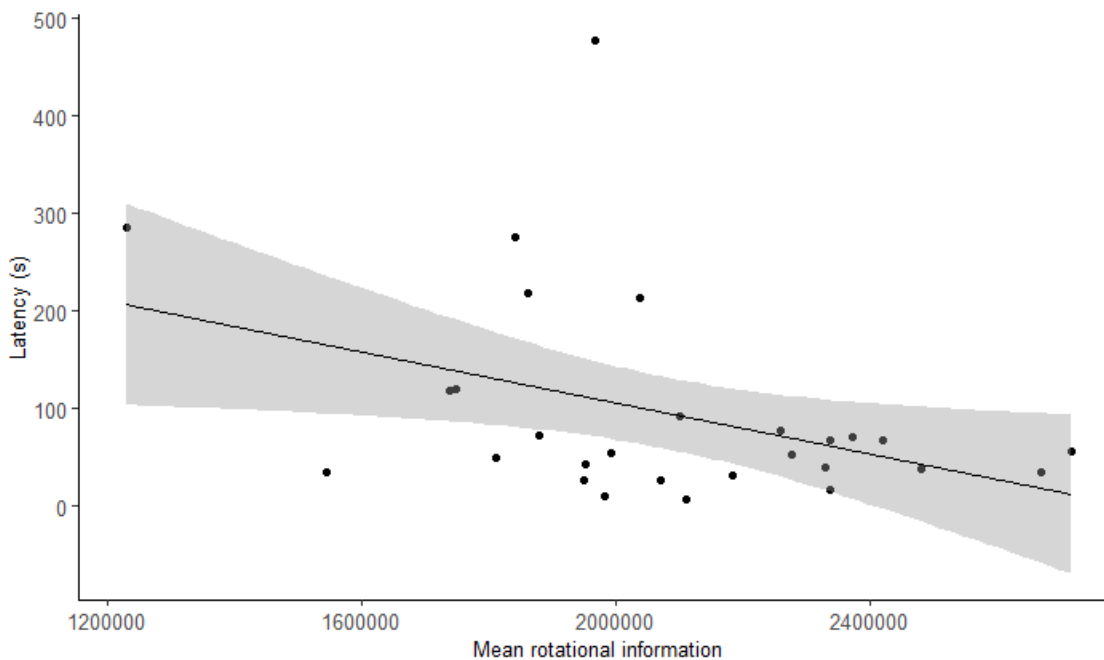
Figure 5. Latency to exit the goniometer by male *O. pumilio*, according to the rotational information available at the displacement site, 8m away from the frog's territory.

Overall, the homing trajectories of male *O. pumilio* that homed successfully were very similar between open areas and the forest (Fig. 6). The mean meander index value was 0.31±0.16, and did not differ between sites (t=1.32, df=10.36, p=0.22). The trajectories showed a high straightness index (0.73±0.015), and did not differ between sites (t=0.16, df=9.91, p=0.88). The mean path length was 11.11±5.90 m, and did not differ between sites (t=-0.51, df=13.95, p=0.62).
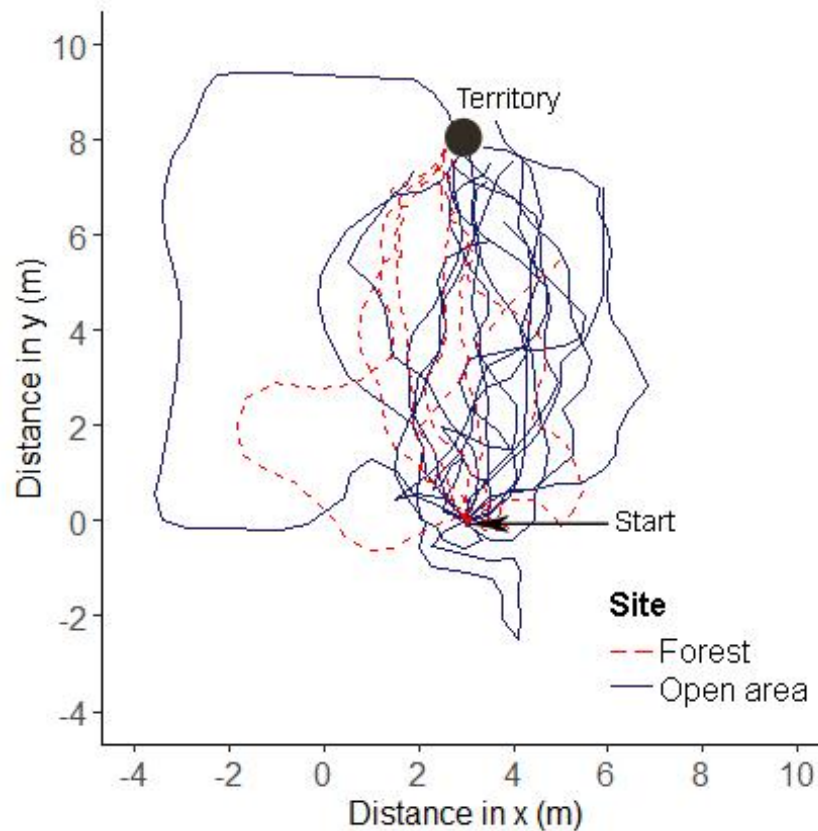
Figure 6. Homing trajectories of male *O. pumilio* that homed successfully after being displaced 8 m away from their territories. Solid blue lines represent frogs displaced in open areas (n = 17) and dashed red lines represent frogs displaced in the forest (n = 7).

We analyzed whether the meander index, straightness index, and path length were predicted by parameters of visual information (rotational information and sky ratio) or the site type (forest vs. open areas). None of the models performed better than the null model (Table 2). However, three models (1) sky ratio, (2) rotational information, and (3) site type performed similarly to the null model (ΔAICc < 2) when predicting meander and straightness indexes (Table 2) and two models (1) rotational information and (2) Site performed similarly to the null model (ΔAICc < 2) when predicting the path length (Table 2). However, none of

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the selected models showed significant effects of individual predictor variables on any of the response parameters (Table 3).

Table 2. Selection of models to predict the characteristics of the trajectories of male *O. pumilio* displaced 8m away from their territories. The Akaike Information Criteria corrected for small sample sizes (AICc) was used to compare models.

Response variable (distribution)	Predictors	AICc
Meander (gaussian)	Sky ratio + Site + Rotational information	-42.42
	Sky ratio + Rotational information	-45.41
	Sky ratio	**-46.93**
	Rotational information	**-47.91**
	Sky ratio * Rotational information	-42.30
	Site * Rotational information	-42.31
	Sky ratio * Site	-42.04
	Site	**-48.10**
	Null	**-48.77**
Straightness (gaussian)	Sky ratio + Site + Rotational information	-9.41
	Sky ratio + Rotational information	-12.61
	Sky ratio	**-14.56**
	Rotational information	**-14.99**
	Sky ratio * Rotational information	-9.46
	Site * Rotational information	-9.69
	Sky ratio * Site	-8.83
	Site	**-14.32**
	Null	-**16.92**
Path length (gaussian)	Sky ratio + Site + Rotational information	-22.43
	Sky ratio + Rotational information	-25.61
	Sky ratio	-27.96
	Rotational information	**-28.43**
	Sky ratio * Rotational information	-22.40
	Site * Rotational information	-22.44
	Sky ratio * Site	-22.37
	Site	**-28.21**
	Null	**-30.58**

Table 3. Results of the models that performed better than a null model when predicting the characteristics of the homing trajectories of male *O. pumilio* when displaced 8 m away from their territories.

Response variable	Model	Predictor	Estimate	z	p
Meander	Model 1	Sky ratio	-0.15	-0.859	0.400
	Model 2	Rotational information	-6.24×10^{-08}	-1.298	0.208
	Model 3	Site (Open area)	-0.0513	-1.370	0.184
Straightness	Model 1	Sky ratio	0.171	0.495	0.626
	Model 2	Rotational information	-7.66×10^{-08}	-0.802	0.431
	Model 3	Site (Open area)	-0.01	-0.167	0.869
Path length	Model 1	Rotational information	4.84×10^{-08}	0.671	0.509
	Model 2	Site (Open area)	0.027	0.491	0.621

We also compared the homing characteristics of successful and unsuccessful males. The initial orientation of males that homed successfully (within the 3hour interval given to perform the task) was territory-directed (Z=0.42, p<0.001, Fig. 7A). In contrast, none of the unsuccessful males showed a territory-directed initial orientation (Fig. 7B). However, the angular error was not different between successful and unsuccessful males (63.35±45.45; t=1.92, df=4.56, p=0.12). The unsuccessful males had a higher latency to exit the goniometer than successful males (unsuccessful: 296±123.85 vs. successful: 62.13±56.00; t=3.71, df=3.21, p=0.03, Fig. 8A).
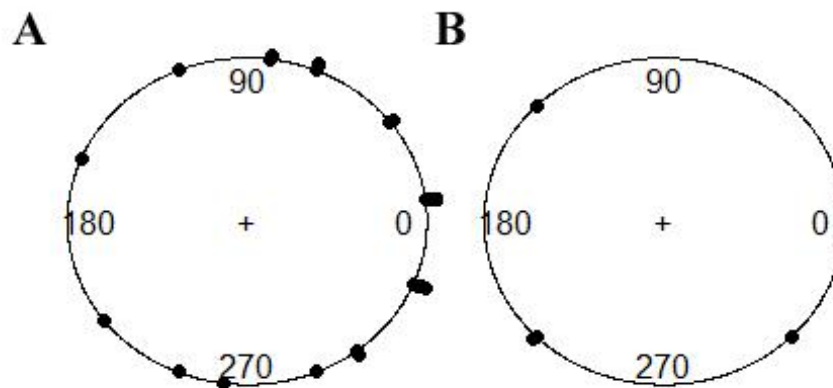
Figure 7. Initial orientation of male *O. pumilio* when displaced 8 m away from their territories that returned successfully or not within 3 hours. **A**. Successful males (n=24) **B**. Unsuccessful males (n=4).
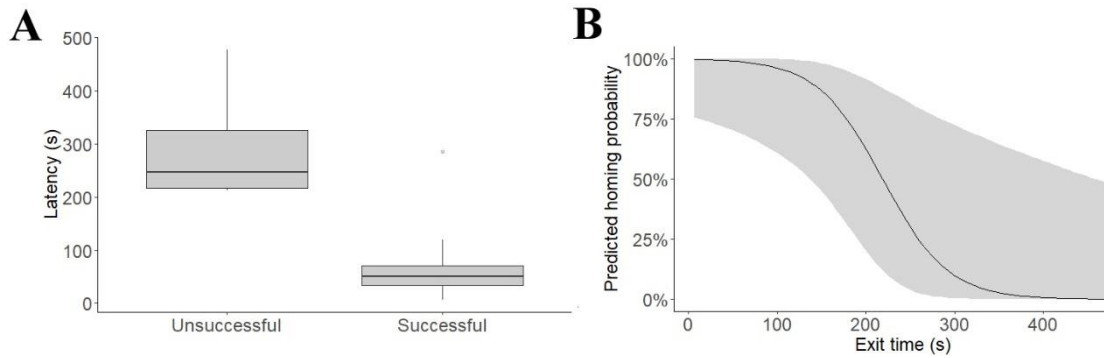
Figure 8. The relationship between homing success and the time taken to exit the goniometer by male *O. pumilio*. **A.** Mean latency to exit the goniometer, according to whether males homed successfully (n=24) or not (n=4) **B.** Probability of homing success according to the latency to exit the goniometer.

The available rotational information was lower at the sites where males failed to home successfully (t=-2.08, df=19.50, p=0.05, Fig. 9A). These sites also had lower sky-ratio values (t=-2.99, df=8.30, p=0.02, Fig. 9B). We performed logistic regressions to test if the rotational information, the sky ratio, or the site type (forest vs. open areas) predicted homing success. We found that two of the models performed better than the null model in predicting homing success (Table 4), but neither model showed significant effects of the individual variables (Table 5). When considering the latency to exit the goniometer as a predictor variable, we found that the time taken to exit the goniometer predicted homing success: frogs that took less time to exit the goniometer also had a higher probability of homing successfully (estimate= -0.02, z=-2.30, p=0.02, Fig. 8B).
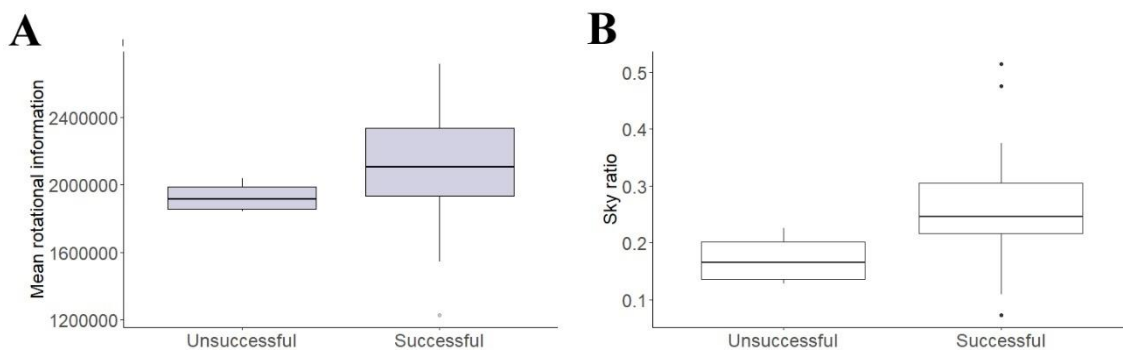
Figure 9. Comparison of the visual information available at the release site, at sites where male *O. pumilio* homed successfully (n=24) and sites where they failed to home successfully (n=4). **A.** Rotational information. **B.** Sky ratio.

Table 4. Selection of models to predict homing success in male *O. pumilio* that were displaced 8m away from their territories. In bold, the chosen model(s) according to the Akaike Information Criteria, corrected for small sample sizes (AICc).

Model	AICc
Sky ratio + Rotational information + Site	**17.47**
Sky ratio	22.66
Rotational information	25.95
Site	**18.42**
Sky ratio * Site	22.13
Sky ratio * Rotational information	19.80
Rotational information * Site	20.90
Sky ratio + Rotational information	24.12
Null	24.97

Table 5. Results of the models that performed better than a null model in predicting the homing success of male *O. pumilio* when displaced 8 m away from their territories.

Model	Predictor	Estimate	z	p
	Sky ratio	4.06×10^{01}	1.414	0.157
Model	Rotational information	-1.11×10^{-05}	-1.578	0.115
	Site (Open area)	2.35×10^{01}	0.004	0.997
Model 2	Site	20.01	0.005	0.996

Effect of canopy- and horizon-based visual information on initial orientation

We displaced 19 males in open areas and manipulated the visual information available at the release site in four conditions (canopy covered, horizon covered, canopy and horizon covered, control). The initial orientation of male *O. pumilio* was not territory-directed in the control, covered horizon, and canopy and horizon covered conditions, but was territory-directed in the canopy covered condition (Table 6). We found that the canopy and horizon-covered conditions showed initial orientation opposite to the territory direction (mean=180°, Rayleigh test, Z=0.349, p=0.01). The angular error was different among treatments overall (F= 3.83, df_1=3, df_2=72, p=0.01). Further comparisons among conditions (Tukey's honest significance difference) revealed that individuals in the canopy-covered condition had lower angular errors than the canopy and horizon covered conditions (p=0.01, Fig. 10A). The latency to exit the goniometer did not differ significantly between conditions (F= 1.41, df_1=3, df_2=68, p=0.25, Fig. 10B).

Table 6. Initial orientation of displaced *O. pumilio* in four different conditions that manipulated the available visual information at the release site. The V test, calculated for each condition separately, evaluates whether the frogs' initial orientation was, on average, territory-directed or not. Significant results are marked with an asterisk (*). Mu =; mean vector, CI = confidence interval.

Condition	V test		Mu (°)	CI (°)
	V	p		
Control	0.313	0.460	85.044	NA
Covered horizon	0.293	0.462	84.242	NA
Covered canopy	5.576	0.035*	57.783	33.094
Canopy and horizon covered	-3.1796	0.8489	117.812	61.645
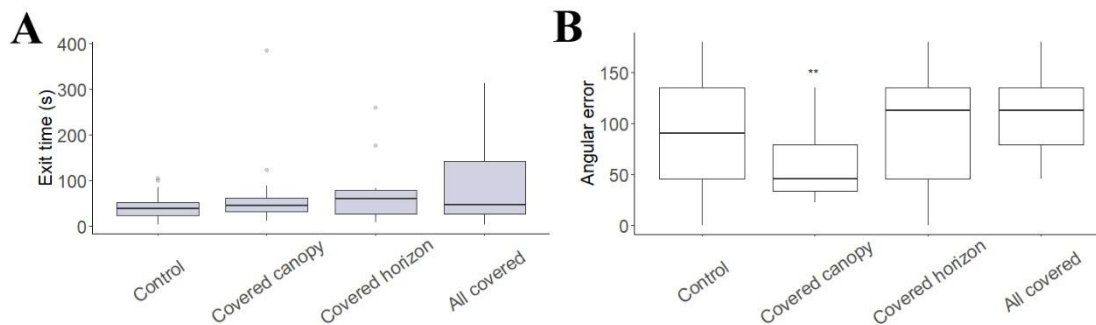
Figure 10. Initial orientation of male *O. pumilio* within four treatment conditions that manipulated the visual information available at the displacement site (control, covered canopy, covered horizon, canopy and horizon covered). **A.** Latency to exit the goniometer. **B.** Angular error of the direction at which the frogs exited the goniometer relative to the true direction of the territory.

DISCUSSION

In this study, we found high homing success within 3 hours by male *Oophaga pumilio* released 8 m away from their territory. The homing success reported here is similar to that found by McVey and colleagues (1981) for males of this species in La Selva. These authors found that 90% of males displaced at 6 m and 12 m successfully arrived home. They did not report the total time of homing, however, our results suggest that *O. pumilio* is able to home relatively quick. (McVey et al 1981). Males of *O. pumilio* showed strong initial orientation towards the territory direction as do as males displaced by McVey and colleagues (1981). High homing success and strong initial orientation has also been reported in other

dendrobatids such as *Allobates femoralis*, *A. talamancae,* and *A. trivittata* (Pašukonis et al. 2013, Pašukonis et al. 2014a, Pašukonis et al. 2014b, Pïchler et al. 2017, Pašukonis 2018).

We found that the quantification of visual information available at the release site via rotational information and sky ratio was successful in showing significant differences between the forest and open areas (Fig. 4). Our initial impression that forest sites seemed to be more visually complex than open areas is supported by these findings, given that forest sites had lower values of both rotational information and sky ratio. Laboratory experiments have shown that dendrobatids with lower complexity of parental care than *O. pumilio* use visual cues to locate targets. For example, using visual landmarks or overall visual configuration to learn the location of a cave, solve a maze or find an immerse platform (Lüddecke 2003, Liu et al. 2016, Liu et al. 2019). Thus, visual information is expected to be of importance for dendrobatid frogs that are navigating through their environment, and for *O. pumilio,* this task appears to be more challenging for individuals navigating in the forest when compared to individuals navigating in open areas.

Our results also showed that the latency to exit the goniometer was predicted by the rotational information available at the release site (Fig. 5), such that less rotational information predicted slower exits. Extended latency to exit the goniometer may reflect the additional time needed to extract the limited visual cues and compare them to memorized templates to determine the direction of the territory. Regardless of exit latency, males successfully homing in open areas were, on average, able to orient towards their territory from the beginning (Fig. 3A). In contrast, males that homed successfully in the forest, where rotational information was lower (Fig. 4), did not initially orient towards their territory. Similarly, when *O. pumilio* was displaced at distances of 25 m, they exhibited higher latencies to leave a platform in the forest than in pasture, and initial territory orientation occurred only in pastures (Nowakowski et al. 2013). Higher latencies are expected as in the forest, visual information changes more rapidly with displacement (Philippides et al. 2011), and the task of recovering the correct direction information is thus harder from 8m.

We found that 100% of frogs in open areas homed successfully, whereas only 65% of frogs in the forest returned to their territories in 3 hours, which is in agreement with our idea that navigation is more challenging in the forest than in open areas. Interestingly, successful males exited the goniometer faster, and lower latency predicted a higher

probability of successful homing (Fig. 7). Males that did not home successfully failed to orient accurately in the direction towards the territory at the release site and were from the forest, which are sites with lower values of rotational information. Lower visual complexity may help males to initially orient quickly and contribute to homed successfully. However, unsuccessful homing refers to males that failed to home within the 3 hours given to perform the task. Three of four unsuccessful males were found back in their territories the day after the experiment, indicating that the homing task was not impossible, but took more time. Together these results suggest that the visual information could play an important during navigation of *O. pumilio*.

The homing trajectories of male *O. pumilio* that homed successfully were very similar between sites, and the shape of these trajectories, which showed accurate orientation, reflects their high homing success (Fig. 9). The lower values of meander index and higher values of straightness index in these routes indicate that the frogs were very well oriented most of the time. However, regardless of the quantifiable differences in visual information between open areas and the forest (Fig. 4), neither the rotational information nor the sky ratio predicted any of the characteristics of the homing trajectories. Lack of effect of visual information on trajectories characteristics may be because the visual information parameters only describe the release site 8 m from the territory, and do not take into account the consistency of visual information between the release site and the territory. If male *O. pumilio* use visual information for initial orientation, they likely also use visual information along the rest of the trajectory. Future studies should quantify visual information and its consistency throughout the trajectory.

Although path length, meander index, and straightness index were similar in the homing trajectories of male *O. pumilio* in open areas and the forest, successful homing took more time in the forest. In both site types, homing behavior was characterized by alternating periods of movement and immobility, but, based on qualitative observations in the forest the periods of were conspicuously longer, as males often hid under the leaf litter along the trajectory. Immobility periods has also been reported during homing of male *A. femoralis* and *A.trivittata*, where frogs could last up to several days without significant movement (Pašukonis et al. 2014a, Pašukonis et al. 2018). Immobility periods are probably influenced by several factors, such as orientation, motivation, stress, weather conditions, and predation

risk (Pašukonis et al. 2018). Sustained periods of movement in open areas could either result from the lack of refuges for hiding or that the frogs were better oriented and knew the direction back to their territory, a distinction that will be important to test in future studies.

Long periods of immobility may be related to the time necessary to perceive cues or accumulate information necessary for orientation in *Allobates femoralis* and *Amereega trivittata* (Pašukonis et al. 2014a, Pašukonis et al. 2018). During the periods of immobility in the forest, frogs occasionally emerged out of the leaf litter for several seconds or minutes before diving back into the leaf litter. Perhaps to accumulate information about the site when conflicting visual information. To determine the role of visual information in the homing trajectory, further studies should ideally manipulate or measure the visual configuration along the trajectory (*i.e.* at sites of immobility and also the territory). Furthermore, accurate descriptions of the immobility periods such as the amount of stopping sites, the time spent in each of them, the visual information available at such sites and their distance from the territory are needed for a better understanding of the role of these periods of immobility in navigation.

In our experiment designed to test the relative role of different visual cues (cues from the horizon *vs.* cues from the forest canopy) only frogs in the canopy-covered condition oriented towards their territories, suggesting that at least the information from the canopy is not necessary for correct initial orientation. Interestingly, frogs in the condition in which both canopy and horizon were covered oriented to the opposite of the territory direction. Contrary to expected, even when the experimental conditions were similar to the experiment in which we tracked the trajectories (particularly in open areas) frogs failed in detecting the correct direction of their territories in the control condition (Fig. 3A). The frogs' disorientation in this experiment may be due to its repeated-measures design, as repeated displacements may have impeded normal navigation behavior back to their territory. Due to randomization, we only tested the control condition first in two trials, whereas the canopy-covered condition was tested first in nine trials whereas the canopy and horizon covered condition was first tested in eight trials. Canopy covered and canopy and horizon covered are the two conditions where we found a mean on the initial orientation. The former, towards the territory and the latter, opposite to the territory. It is possible that after the first trial, frogs avoided exiting in the same direction in subsequent trials to prevent capture. However, when analyzing only the

first trial of each male we failed to find any significant difference between trials, likely because of very low sample sizes per condition. The results of this experiment would be better interpreted by testing each frog only once in each of the test conditions.

The homing trajectories and behavior of male *O. pumilio* described here is similar to that reported for other dendrobatids, which may be associated with familiarity with local cues. Male *A. femoralis* have higher homing success when displaced into familiar sites suggesting that they rely on experience with local cues to navigate (Pašukonis et al. 2014b). We displaced *O. pumilio* males only 8 m away from their territory, and the home range of males at La Selva ranges from 2.26 to 15.07 m^2 (Donnelly 1989). Unfamiliarity with the site of displacement could explain the lower homing success of *O. pumilio* in La Selva reported by Nowakowski et al. (2013), who reported a decrease in homing success with distance, from 67% at 20 m to 57% at 30 m after 2 weeks (because they released the frogs and checked the site every for 3 minutes only, it is likely that the time required for successful homing was overestimated in their study – it is known that even frogs holding a territory are not always at the same site when the territories are inspected (Donnelly 1989, Nowakowski et al. 2013). Nowakowski and collaborators (2013) did not differentiate between homing success of male and female frogs. Female home ranges at La Selva are slightly larger than those of males, from 5.72 m^2 to 15.11 m^2 (Donnelly 1989) but still smaller than displacement distances in this and other studies (Nowakowski et al. 2013). Because it is unlikely that home ranges are circular, unfamiliar release sites are more likely across 8, 20 or 30 m of displacement and could influence differences in homing success across studies.

There is still little understanding of the nature of the cues used by dendrobatids during navigation. Female *O. pumilio* and male *A. femoralis* recognize tadpole deposition sites based on local cues (Ringler et al. 2013, Pašukonis et al. 2016, Beck et al. 2017, Stynoski 2009, Ringler et al. 2016). In other dendrobatids, like *Ranitomeya variabilis*, females use chemical cues to recognize tadpoles in phytotelmas (Schulte et al. 2011). Visual cues also are part of a multimodal sensory integration (along with chemical and tactile cues) that triggers begging behavior in tadpoles of *O. pumilio* (Stynoski & Noble 2011). Future studies should be aimed at understand the processing of visual information in dendrobatids, and how that processing could influence navigational abilities, especially concerning parental care behaviors (Fisher et al. 2019). It is also important; we need to understand how and if visual information is

integrated with other sensory modalities. Due to the variety and nature of the cues in the environment, a diversity of sensory systems would improve navigation through a better representation of the environment (Ferguson 1971, Narins 2005, Wystrach & Graham 2012, Hoinville and Whener 2018, Kugler 2019). Future manipulative experiments coupled with a study dedicated to sensory processing in frogs would be useful to clarify how poison frogs integrate environmental cues during their daily navigation.

CONCLUSIONS

- Overall, the homing success of male *O. pumilio* was high, with higher success in open areas when compared to the forest, which implies that the navigational task is more demanding in the forest.
- As originally expected, the forest was visually more complex than open areas, with lower rotational information and sky ratio.
- Lower visual complexity (high rotational information and sky ratio) at the release site predicted faster exit times from the goniometer, suggesting that visual information may play a role in determining the initial orientation.
- The homing trajectories in the forest and open areas were very similar; males traveled almost in straight-lines, showing strong orientation along the trajectory. However, in the forest males took more time, adding support to the idea that the navigational task is more challenging in the forest.

RECOMMENDATIONS

- To better understand the role of visual information during homing future studies should quantify visual information and its consistency throughout the trajectory.
- Precise descriptions of the behavior of frogs during immobility periods such as the amount of stopping sites, the time spent in each of them, the visual information at these sites and their distance from the territory could help interpret the role of this behavior during navigation.
- For reliable results about the role of visual cues from the horizon vs. visual cues from the canopy during initial orientation, the experiment performed here could be improved by testing each frog only once in one of the conditions.

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ANIMAL ETHICS

All experimental procedures were approved by the Comité Institucional para el Cuidado y Uso de los Animales (CICUA) from the Universidad de Costa Rica, under the permit number CICUA-056-2019.

RESEARCH PERMIT

The fieldwork was done under the permit of the National System of Conservation Areas SINAC-ACC-PI-R-090-2019.

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