



# Ecological and behavioral correlates of homing performance in the egg-feeding poison frog *Oophaga histrionica*

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## Abstract

Homing is the ability to return to previously visited sites, often to the home range. Most studies have focused on the mechanisms used to home, but few have addressed the cost-benefit analysis of homing behavior, e.g., by testing for associations between homing performance and ecological factors. We aimed to study homing ability in males of the poison frog *Oophaga histrionica*, by testing the general hypothesis that homing performance depends upon potential indicators of territory quality or the risk of losing it. First, we tested whether return time was related to displacement distance, body size, number of courtships during the previous month, or distance to nearest neighbors. 38 out of the 39 displaced males homed, and time to return was inversely related to displacement distance, yet not related to any of the other ecological variables tested. In a second experiment, we tested whether males' homing performance was affected by adding or removing acoustic cues, to simulate changes in the number, identity, and spatial distribution of neighbors. All of the 41 displaced males homed; 78% homed within six hours, and the remaining 22% returned after six hours. Among the former, males exposed to additional loudspeakers (e.g., neighbors) within their territories and to a loudspeaker broadcasting from their very calling perch (replacement treatment), were found significantly closer to the capture site than males in other treatments. Our results thus indicate that the homing performance of males is affected by the perceived risk of being displaced from their territories.

**Keywords** Acoustic cues · *Dendrobates* · Homing · Poison frogs

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## Introduction

Space use and spatial distribution differ in animals depending on ecological requirements and life history strategies. Individuals may also make differential use of space by moving between different sites, where they find the resources needed according to their life history stage (e.g., juvenile or adult) or their motivational state (e.g., hungry, or reproductive). As spatially separated resources change in abundance and predictability (e.g., there is depletion of food, mates, or shelter sites), individuals may return to previously exploited sites using behavioral mechanisms that have been described in the scientific literature as homing (Papi 1992). Animals appear to home by using a wide range of cues (e.g., visual, chemical, magnetic, and acoustic cues) depending on the displacement distance, the time of day when they travel, and the general habitat (e.g., aquatic versus terrestrial); overall, most animals appear to use more than one type of cue to home (Ferguson 1971; Papi 1992; Sinsch 2006).

Homing ability should be higher in species with high site fidelity (e.g., territorial species) and species with parental care, especially if resources are spatially segregated (McVey et al. 1981; Crump 1986; White and Brown 2013; Gould et al. 2014; Levasseur et al. 2021). In amphibians of the order Anura (frogs and toads), homing behavior has been reported in species from various families, such as Hylidae, Bufonidae, Ranidae, Centrolenidae, and Dendrobatidae (McVey et al. 1981; Crump 1986; Lüddecke 1996; Pašukonis et al. 2013; Pichler et al. 2017; Navarro-Salcedo et al. 2022). Because all studied neotropical poison frogs (Dendrobatoidea) species are territorial and exhibit parental care (Pröhl 2005) homing is a widespread and well-developed behavior within this taxon. Homing behavior has been reported in several species of dendrobatid frogs, such as *Oophaga pumilio* (McVey et al. 1981; Nowakowski et al. 2013), *Allobates femoralis* (Pašukonis et al. 2013), *Allobates talamancae* (Pichler et al. 2017), *Ameerega trivittata* (Pašukonis et al. 2018; Nothacker et al. 2018), *Andinobates bombetes* (Arcila-Pérez et al. 2020), *Oophaga sylvatica* and *Dendrobates tinctorius* (Pašukonis et al. 2022).

In dendrobatids, homing success tends to be lower in individuals that are displaced longer distances, as has been shown in *A. trivittata* (Nothacker et al. 2018), *O. pumilio* (McVey et al. 1981), *A. femoralis* (Pašukonis et al. 2013), *A. bombetes* (Arcila-Pérez et al. 2020) *A. talamancae* (Pichler et al. 2017). This could be because travel costs become too high or because the individual lacks the necessary information to home (Sinsch and Kirst 2016). However, not all species of anurans exhibit lower homing success at higher displacement distances (*Ikakogi tayrona*, Navarro-Salcedo et al. 2022).

Given that the parental behavior of species of *Oophaga* requires both tadpole transportation and egg feeding, they provide an interesting opportunity to understand the ecological and behavioral correlates of homing behavior, since the movement in both sexes may be limited by these two factors. In *O. pumilio*, both males and females home, males are territorial, and parental care is carried out by females, which consists of transporting terrestrially hatched larvae to water-filled bromeliads, and then providing them with nutritive, unfertilized eggs during their development (Weygoldt 1980). In *O. sylvatica*, males are not engaged in parental care and have a smaller home range than females, but they do not differ in their navigational performance. Though males and females travel similar daily distances, males move mostly within their territories; however, when translocated, they tend to explore their surroundings more than females do (Pašukonis et al. 2022). Similar patterns of territorial behavior and parental care occur in *O. histrionica* (Zimmermann and Zimmermann 1981;

Summers 1992; Summers and Earn 1999) a species from the Pacific lowlands of Colombia, which is closely related to *O. pumilio* and to *O. Sylvatica* (Silverstone 1973; Myers and Daly 1976; Grant et al. 2006).

Males of *O. histrionica* aggregate in discrete patches and actively defend (Méndez-Narváez and Amézquita 2014) multipurpose territories; in a closely related species, *Oophaga sylvatica*, territory size ranges from 2 to 66 m<sup>2</sup> and encompass display perches as well as oviposition sites, yet probably not the phytotelmata used by females for deposition and feeding of larvae (Summers 1992). Based on the spatial distribution of resources, the high density and contiguity of territories, and the conspicuous aggressive reaction of territorial males towards intruders, we predicted that males should exhibit well-developed abilities to return to their territories if displaced from them (i.e., they should home), and that return time (homing performance) should depend upon ecological factors that affect the costs and benefits of homing. We used correlative and manipulative experiments to test the following predictions: (1) homing success should be lower in males that are displaced longer distances because travel costs become too high or because the male lacks the information necessary to home. (2) Males that experienced high courtship success at their territories should predictably home and should return sooner because good-quality territories increase the benefit of homing and the costs of losing the territories to other males. (3) Males that hold territories very close to other territorial males should predictably home and should return sooner, because high male density may increase the risk of losing females or losing the territory to other males. (4) Male body size should affect homing performance because body size may influence the probability of regaining a territory occupied while the male was away. Finally, (5) changes in the acoustic environment should affect homing performance because the acoustic environment (i.e., the number and distribution of calling neighbors) may indicate the risk of losing the territory to other males or it may provide directional cues.

## Materials and methods

### Study system

The study was conducted during July–August 2006 and June 2007 at El Amargal Biological Station, near Arusí, Chocó, Colombia (5°34' N, 77°30' W, between 60–120 m.a.s.l.), which the NGO Fundación Ingedé privately owns. At the study sites, males of *O. histrionica* are found calling from fallen trunks and roots, more often as discrete aggregations of contiguous territories of about 30–70 males. Aggregations appear more common at the clearings of the relatively undisturbed tropical rainforest. Due to the high (around 8000 mm/yr) and almost continuous precipitation, the calling activity appears extended throughout most of the year. We conducted our experiments on territorial males (i.e., males that were calling for several days) from two breeding aggregations, separated by about 1.7 km.

To estimate the precise location of individual frogs, we first laid out a physical grid of about 96×144 m<sup>2</sup>, subdivided into squares of 8×8 m<sup>2</sup>, throughout the study area, and marked by placing flagging tapes at each corner of the 8×8 squares. A male found within an 8×8 m square was always mapped against the square corners using a compass and a measuring tape, to render an estimated precision of 1 m<sup>2</sup>. To census territorial males, 1–2 people searched daily for calling individuals, between 0730 and 1600 h. Because only males call

in this species, male frogs were identified by observing spontaneous calling activity or by capturing and gently handling them to evoke release calls, which females lack. The distinctive dorsal and lateral color patterns were drawn both on plastic cards in the male's territory and on a field notebook and used to identify each male. Photographs were also taken of each male. The location of the plastic card was also recorded on a map with a scale of 1 cm:2 m to represent the  $96 \times 144 \text{ m}^2$  grid we had set up on site. The plastic cards from the first field season (2006) were evaluated and compared against the male found calling from the territory in the second season (2007). The distance between the place where the plastic cards were initially placed and where the males were located in the second season were recorded, to estimate inter-seasonal territory holding.

### Ecological correlates of homing performance

A first homing experiment consisted of capturing an already known male and displacing it from the capture site inside an opaque (black) plastic bag, to minimize visual or chemical cues that might provide information to the frog about the displacement direction. A total of 39 males were displaced either 10 m ( $N=13$ ), 25 m ( $N=13$ ), or 40 m ( $N=13$ ) away from the capture site and were randomly assigned to an eastward or westward translocation. They were then released on the forest floor, by opening the plastic bag, so that they could come out and start moving at any time. We searched for displaced males during daily censuses around the entire plot, both looking for and listening for calling males. Homing performance was measured by estimating return time as the number of days (at 0.5 d precision) elapsed between the moment of release and the moment when it was found back in its territory, i.e., within 2 m of the capture site.

To estimate body size, we measured the snout-to-urostyle length of each male on scaled digital pictures with the software Carnoy for Macintosh OS X (<http://bio.kuleuven.be/sys/carnoy/>). To estimate courtship success, we looked for courting males during daily censuses, i.e., males found (mostly calling and visually displaying) with 20 cm of a female. Courtship success of each male was then estimated as the number of females courted, after ruling out covariation with the number of days it was looked for. To estimate the distance to neighboring territorial males, we identified the location of encounter sites during daily censuses and plotted these positions on the map mentioned in the study system. We then constructed convex polygons on the map, by connecting the furthest points where each individual was found and measured the distance from the polygon's centroid to the corresponding centroids of the three nearest neighbors. Displacement distance, body size, courtship success, and distance to neighbors were then used as potential predictors of return time in graphical and statistical analyses. The output variable, return time, was transformed using the inverse function ( $1/\text{SQR}(y+1)$ ) to achieve normality, before building and testing a generalized linear model. Alternative models were tested without transforming the output variable and assuming other distribution families (Gamma, Poisson and Gaussian), but all of them rendered model deviance values at least two orders of magnitude higher than the chosen model.

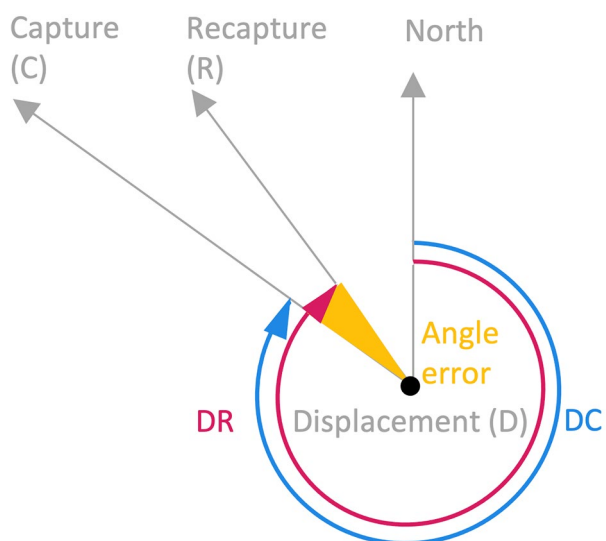
### Acoustic environment and homing performance

To test whether changes in the number and the spatial distribution of neighboring territorial males affect homing performance by *O. histrionica* males, we manipulated the acoustic

environment either inside the territory or in the surrounding area of focal males. Every day, between 0800 and 0930 h, 2–4 people searched for calling males, captured 2–4 males/day, and displaced them 10 m from the capture site in a randomly chosen direction (east or west). We chose 10 m as the displacement distance because the first experiment (see above) had shown that males are able to home from 10 m within a few hours, and because restraining the experiment to one day reduced variation in return time due to eventual nocturnal traveling. Six hours after releasing males, the same group of people carefully searched for displaced males within an area of at least 314 m<sup>2</sup> around the capture site. This area was determined as the area of a circle of radius 10 m (the displacement distance). Since all males were captured while they were calling, the capture site was assumed to be part of the territory. After locating a male, its position was recorded (angle and distance) in relation to the original capture site. Consequently, the output variables for this experiment are travel distance and angle error, the latter expressed as the difference between the expected direction (the direction from capture to release site) and the actual travel direction (Fig. 1).

The acoustic environment was modified by simulating new territorial males with acoustic playbacks, and by modifying their number and their position in relation to the focal male. By combining the addition of simulated males with the replacement of usual neighbors, we attempted to discriminate between two possible roles of the acoustic environment on homing performance: to indicate the risk of losing the territory to other males and to provide acoustic cues for spatial orientation during homing. Accordingly, experimental males were assigned to each of the following treatments: (a) Replacement: an acoustic stimulus was played back from the capture site of the displaced male; it simulates a situation in which the focal male's territory was taken over by another male (N=9 males). (b) Neighbor's identity: two acoustic stimuli were played back from the calling positions of the two nearest neighbors, which were temporally removed from the area; it keeps providing information on neighbor's position but alters information on neighbor's identity (N=9). (c) Neighbor's density: an increase in the number of neighbors was simulated by playing back two acoustic stimuli from randomly chosen positions within 7 m of the capture site of the tested male, and

**Fig. 1** Calculation of angle error. Male frogs were captured at site C and displaced to site D. The angle (from North) to the capture site was recorded as DC (blue circle). Males were then recaptured at R. The angle (from North) to the recapture site was recorded as DR (pink circle). The angle error (yellow wedge) was measured as the difference between DR and DC.



without removing any neighbors; it simulates an increase in the risk of losing the territory to other males ( $N=11$ ). And (d) Control: the male was displaced without adding or removing any acoustic cue ( $N=12$ ).

Acoustic stimuli were digitally synthesized by using temporal and spectral characteristics of *O. histrionica* advertisement calls, previously recorded in the field (Erdtmann and Amézquita 2009). On average, the natural range of calling rate is  $3.026 \pm 0.234$  calls/sec, calls last  $164.51 \pm 25.3$  ms (mean  $\pm$  SD) and consist of  $48 \pm 13$  pulses, uttered with a dominant frequency of  $2.888 \pm 0.145$  kHz (Gil-Guevara and Amézquita, 2020). In this experiment, synthetic calls were emitted at a rate of  $3.026 \pm 0.234$  calls/sec, with a mean intensity (SPL) of  $76.6 \pm 1.34$ . To avoid pseudoreplication of acoustic treatments (Kroodsma 1989, 1990), we never used the same call in two experiments. Call replicates were prepared by randomly modifying call parameters within  $\pm 1$  standard deviations of the average (Amézquita et al. 2005, 2006). Calls were stored as mp3 files in memory cards and played back from Verbatim Smartdisk 95,456 MP3 players through Sony SRS\_M30 loudspeakers. The acoustic stimuli were broadcast from the time of release to the time of recapture at rates within the natural range of variation of call rate at the study site.

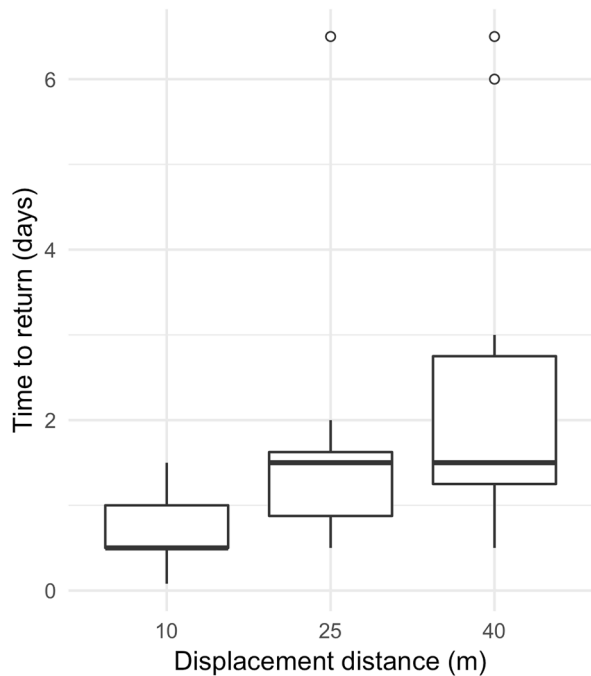
Data on angle error were analyzed using parameter estimation for circular data. In particular, we estimated mean angle errors, and the corresponding 95% confidence intervals by resampling the original data set 999 times assuming a von Mises circular distribution (Batschelet 1981) on the *CircStats* R package (Lund et al. 2018). To estimate the homing performance, we first checked whether confidence intervals included the expected 0 degrees direction, and to compare pairwise experimental treatments we examined whether there was overlap between the corresponding confidence intervals. To graphically depict the mean travel direction for males within each experimental treatment, we estimated an  $r$  vector of mean travel direction using both angle errors and straight travel distances.

## Results

75% of males were found within 2 m of the calling site where they had been captured a year before. 79 out of the 80 displaced males in both experiments homed. 97% ( $N=38$ ) of displaced males in the first experiment homed, independent of body size ( $X=77.7 \pm 6.4$  mm), distance to nearest neighbor ( $X=14.2 \pm 6.7$  m), or number of courtships ( $X=0.97 \pm 0.84$  courtships). In the first experiment, all homing males returned within 0.5–6.5 d, and there was a significant effect of displacement distance on time to return (GLM,  $t=-2.697$ ,  $p=0.0117$ ,  $n=36$ , Figs. 2 and 3). Males that were displaced shorter distances away from the capture sites returned slightly sooner than those displaced longer distances. Males homed equally fast independent of previous courtship success ( $t=0.727$ ,  $p=0.4732$ ,  $n=32$ , Fig. 3), distance to nearest neighbors ( $t=0.266$ ,  $p=0.7922$ ) or body size ( $t=0.001$ ,  $p=0.9992$ , Fig. 3).

In homing experiments where the acoustic environment was manipulated, all 41 displaced males homed. 78% of males were recaptured within 6 h after displacement and there was no significant difference between treatments in the number of recaptured males (Chi-squared test:  $\chi^2=5.934$   $p=0.204$ ,  $n=32$ ). The remaining 22% were found at their place of capture after 6 h but were not included in the analysis to avoid introducing noise in travel time due to the absence of the researchers at the study site upon the males' return to their territory.

**Fig. 2** Relationship between displacement distance and time to return by males of *Oophaga histrionica*. Time to return is estimated as the number of days from the release of males to the recapture. The box represents the middle 50% of the data, with the interquartile range (IQR) being the distance between the lower and upper quartiles. The whiskers extend to the most extreme data points that are not considered outliers. Outliers are data points that are more than 1.5 IQRs away from the nearest quartile. Empty circles represent outliers from the normal distribution of the data

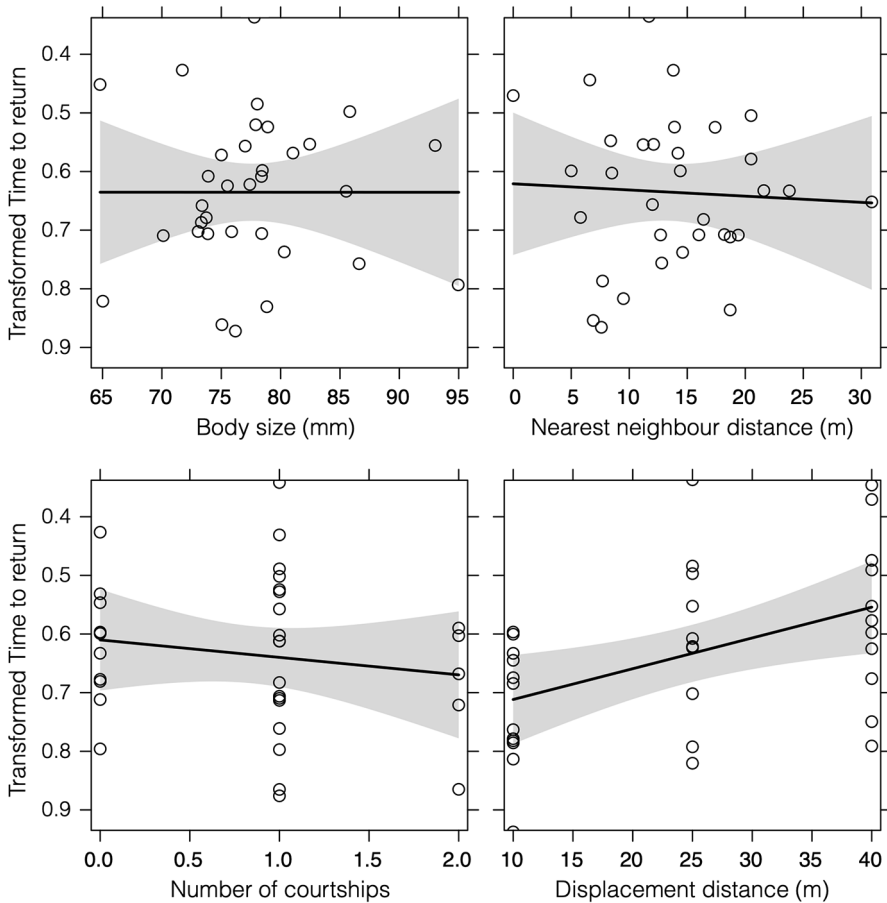


Recaptured males were found within 0–10 m from the capture site. Those from the control treatment were found more scattered and comparatively away from the expected 0 degrees direction (-18.9 degrees, -40.8 to 5.8 degrees, mean and 95% confidence interval, Fig. 4), followed by males in the neighbor's identity treatment (-8.7, -16.8 to -0.8 degrees). In contrast, males were found relatively closer to the expected 0 degrees direction in the replacement (-6.5, -20.2 to 3.7 degrees) and neighbor's density treatments (-1.8, -12.6 to 10.3 degrees). Males in the replacement treatment, where the acoustic stimulus had been set up at the male's original calling site, were recaptured on top of the speaker 38% of the time, compared to 0% in other treatments.

## Discussion

As predicted, males of *O. histrionica* were clearly able to return when displaced away from their territories. In the first experiment, all males homed successfully within 0.5–6.5 days, and return time was significantly shorter for males displaced shorter distances. Against our expectations, return time was not correlated with previous courtship success, distance to nearest neighbors, or body size. When the acoustic environment was manipulated, males' homing performance was better (i.e., they exhibited lower variation in the angle error) than males in the control treatment, especially when the position of the focal male was occupied by a simulated intruder.

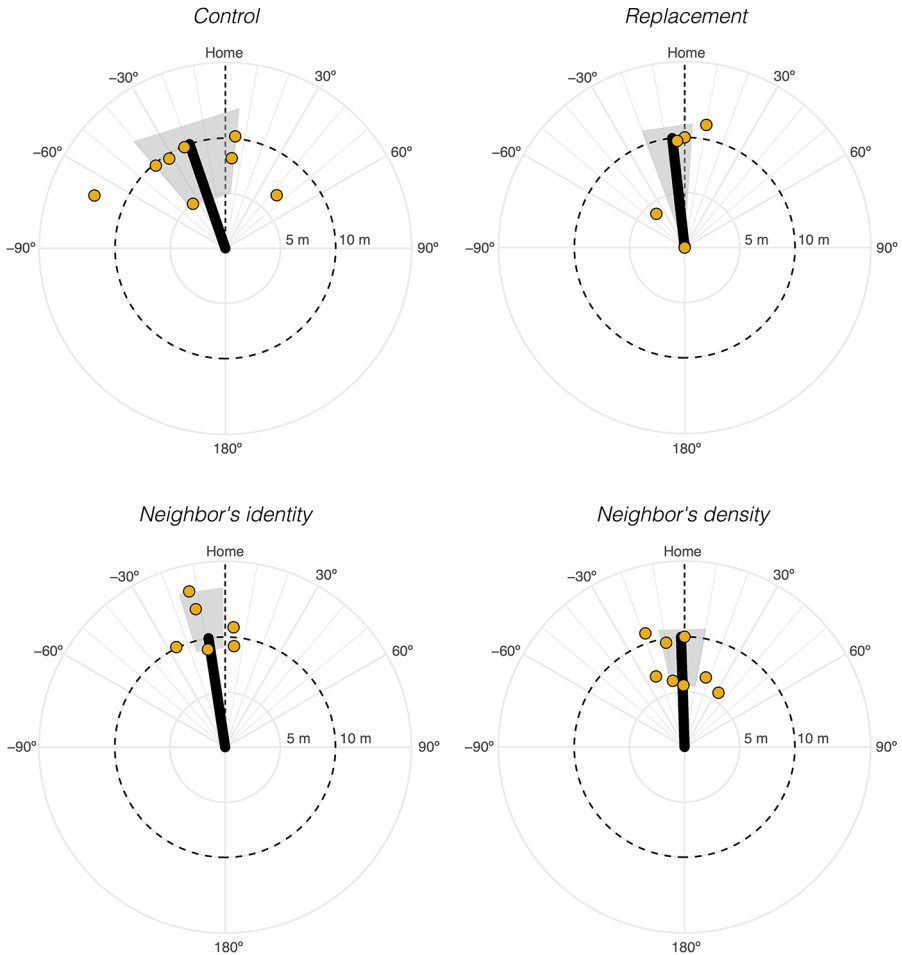
In our first experiment, 92% of males of *O. histrionica* returned to their territories from 40 m away, and 100% of males returned from 10 to 25 m. Based on previous studies in



**Fig. 3** Partial effects plot of the relationship between homing performance (transformed time to return) and body size, average distance to the three nearest neighbors (NND), previous courtship success, and displacement distance in males of *Oophaga histrionica*. Time to return is estimated as the number of days from the release of males to the recapture and was transformed by the function  $(1/\text{SQRT}(y+1))$ . We reversed the axis to improve the readability of data; therefore, larger values in the Y axis denote longest time to return

neotropical poison frogs, this percentage is one of the highest recorded, only comparable to Pašukonis et al.'s (2013) experiments, where 87% of males of *A. femoralis* homed from 200 m away from their territory (estimated to be around 13.9 m in diameter). In terms of distance, the maximum homing distance reported for dendrobatids is in *A. trivittata*, which returned after being displaced 900 m (Nothacker et al. 2018). The distance covered by *O. histrionica* in this study is comparable to that of *O. pumilio* (30 m, Nowakowski et al. 2013) *O. sylvatica* (50 m, Pašukonis et al. 2022) and shorter than that of *A. bombetes*, 90 m, (Arcila-Pérez et al. 2020), *D. tinctorius* and *A. femoralis*. It is also shorter than that covered by frogs of other families, such as the centrolenid *Ikakogi tayrona*, 320 m, (Navarro-Salcedo et al. 2022). Nowakowski et al. (2013) found that only 57% of translocated *O. pumilio*





**Fig. 4** Homing performance of male *Oophaga histrionica* displaced 10 m away from their territories, under one control and three experimental treatments. Data points denote travel distance (magnitude) and angle error, i.e., the difference between the expected (arbitrarily set at 0° and representing the capture site) and the actual travel direction for individual frogs. Travel distance is then denoted as the distance from the center of the Fig. 0 m would represent no travel distance between the place where the male was captured and where it was recaptured. The average vector is dark grey and its magnitude (between 0–1) is described by rho. The distance of the dots to the center was not used for the calculation of the mean vector. The confidence intervals for the mean vector are shown in light grey

homed from distances up to 30 m. Pašukonis et al. (2022) that found in *O. sylvatica* 80% of translocated males and 70% of displaced females homed from distances of up to 50 m.

It may be that the egg-feeding behavior in *O. pumilio*, *O. sylvatica* and *O. histrionica* restricts them to shorter home ranges than those found in *A. femoralis*. However, this behavior is likely to vary by sex: in *O. sylvatica*, males had a smaller home range than females, who perform parental care; females also moved more on days of parental care (Pašukonis et al. 2022). Nevertheless, the question remains of why (and how) they home at all from such distances if they do not usually travel that far.

Though the size of the territory in *O. histrionica* is unknown, the estimated territory size of male *O. sylvatica*, which is phylogenetically close to *O. histrionica*, is 3.9 m<sup>2</sup> in an Ecuadorian population (Summers 1992). In this study, travel distance within the territory can be roughly estimated as half the average distance to the nearest neighbors: 5 m. Thus, males displaced 10 m away from their calling sites may have returned significantly sooner because they traveled in familiar areas, close to or within their territories, whereas males displaced 20–40 m away from their calling sites took a longer (or similar) time to return. Though returning from 10 m takes less time than returning from 20 to 40 m, it is surprising that there was no significant difference in return time from 20 to 40 m. This may be because they were further outside their territories, and hence lacked the cues to guide them directly home, or because they took their time exploring new sites, as males of *O. sylvatica* do (Pašukonis et al. 2022).

Another source of evidence suggests that male *O. histrionica* do not travel long distances once they establish their territories. Territory holding is prolonged, at the study population: in the course of this study, 75% of males were found within 2 m of the calling site where they had been captured a year before; males that were not found at their previous-year territory were found on neighboring territories that belonged to another male in the previous year. Other dendrobatids exhibit site fidelity for up to two or three breeding seasons (Roithmair 1994; Pröhl and Hödl 1999). However, the median displacement in other species is higher. In *A. femoralis*, the median inter-year displacement was around 28 m (Ringler et al. 2009). Both the small territory size and the low turnover rate indicate that naturally occurring travel distances are rather short, compared to homing distances in male *O. histrionica*. They also pose interesting questions on males' ability to use environmental cues for beaconing, piloting, or navigation, and to retain the information acquired before the establishment of territories (e.g., in pre-maturational stages).

Against our expectations, homing performance was not correlated with previous courtship success, distance to nearest neighbors, or body size. Our initial predictions assumed that homing is costly and, therefore, homing performance should be correlated with environmental or intrinsic indicators of homing benefits and costs. Benefits of territory quality could be estimated from a high mating rate or low male density, whereas costs could be related to the risk of returning to an occupied site (as estimated from male density) and not being able to defend it (as estimated from body size). That environmental or intrinsic factors do not correlate with homing performance could be explained by the strong site fidelity of male *O. histrionica*. As explained above, territory holding appears to be very prolonged and the territory turnover rate is concomitantly low. In addition, there was little among-males variance in the number of courtships during the previous month (most males only had 1 courtship), supporting that high site tenacity may grant territorial males access to a similar number of females. Thus, the males' priority would be to return as soon as possible to their territories, regardless of intrinsic or environmental information available on territory quality.

The effect of the acoustic environment on males' homing performance suggests that acoustic cues are used to estimate the risk of losing territory to other males, rather than to orient themselves during the travel. Compared to control experiments, males were found closer to the expected travel direction when additional calling males were simulated within their territories or at their very calling perches. In the replacement treatment, when the acoustic stimulus had been set up at the male's original calling site, males were recaptured on top of the speaker 38% of the times, compared to 0% in other treatments. Thus, although males' homing performance did not

correlate with the distance to nearest neighbors in the first phase, it was indeed affected by the simulation of other males in their territory by acoustic playback in this experiment. The contrast indicates that males use local cues rather than previous experiences in estimating the risk of losing their territories and in modulating their homing behavior.

On the other hand, changing the identity of neighbors, in an attempt to disorient homing males, did not result in lower homing performance, compared to the control treatment. Manipulating neighbor's identity should negatively impact homing by males of *O. histrionica* only if they are able to use acoustic cues to discriminate between neighbors and strangers, as has been shown to occur in *Rana catesbeiana* (Davis 1987) and *Colostethus beebei* (Bourne et al. 2001). In fact, Bee (2003) and Gardner and Graves (2005) failed to find support for neighbor-stranger discrimination in the closely related species *O. pumilio*. Although our experiment was not designed to test neighbor-stranger discrimination, it clearly indicates that information on neighbor's identity (as estimated from acoustic cues) is either unavailable (due to males' lack of perceptual ability) or irrelevant for orientation, at least at the spatial scales (10 m) in which we conducted our experiment. Nevertheless, since males of some frog species use chorus calls or river sounds to home (Gonser and Woolbright 1995), we cannot discard the usefulness of acoustic information for orientation during homing travels.

In sum, our study shows that males of *O. histrionica* extend their homing ability beyond the range of their territories and that homing performance is modulated by the actual acoustic environment (the presence of other males at their territory) rather than by recent experience on courtship success or neighbors' density. The results are consistent with a scenario of strong site fidelity and a low rate of territory takeovers in which holding territory is valuable enough to justify homing. However, the mechanisms underlying these homing abilities as well as the criteria used to select the territories remain unknown.

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**Author contributions** Both authors contributed to the study conception and experimental design. Data collection and analysis were carried out by Juliana Gómez-Consuegra. The original version of this manuscript was written by Juliana Gómez-Consuegra. Funding acquisition was done by Adolfo Amézquita. Visualizations were done by both authors. All authors worked on, read, and approved the final manuscript.

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**Data availability** The datasets generated and analyzed during the current study are available on the DRYAD repository (doi:<https://doi.org/10.5061/dryad.44j0zpc3>).

## Declarations

**Ethics approval and consent to participate** Ethics approval was granted by the Faculty of Sciences of the University of Los Andes, under code 280–2006/02-BIO01, when the project was assessed as “Riskless research”.

**Competing interests** The authors have no relevant financial or non-financial interests to disclose.

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