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Homing performance in a territorial dendrobatid frog, *Allobates talamancae*

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Many amphibians show high site fidelity (Sinsch 2014) and are able to find their way back after experimental translocations (reviewed in Sinsch 1990). Such homing ability has been studied mostly in nocturnal temperate region amphibians (e.g., *Anaxyrus terrestris* [Bufonidae] [Bogert 1947], *Lithobates pipiens* [Ranidae] [Dole 1968], *Pseudacris regilla* [Hylidae] [Jameson 1957], *Taricha rivularis* [Salamandridae] [Twitty et al. 1964]), where individuals seasonally move between fixed breeding sites and hibernation sites. While it is well established that many amphibians are capable of homing, comparative data of homing performance in different species is scarce. Estimations of recapture potential without translocation or the use of tracking devices are essential for reliable estimates of homing time and success. However, most homing studies in amphibians lacked appropriate control groups to estimate recapture potential and did not track the animals after translocation. As a result, reliable data of homing performance are lacking for most amphibians.

Tropical amphibians show extremely diverse reproductive and spatial behaviours, such as long-term territoriality and long-distance movements between fluctuating breeding sites. However, homing ability has rarely been studied in tropical species (but see Gonser & Woolbright 1995, Nowakowski et al. 2013, Pašukonis et al. 2013, 2014a, b). Poison frogs (Dendrobatidae) are a group of small diurnal Neotropical frogs that show some of the most complex spatial behaviours among amphibians. Dendrobatid frogs are characterised by territoriality and tadpole transport from terrestrial clutches to widely scattered aquatic deposition sites (Weygoldt 1987). Many poison frogs rely on homing as the water bodies for tadpole development are often situated outside their territory (e.g., Roithmair 1994, Ringler et al. 2009). Homing ability after experimental translo-cation has been studied only in the strawberry poison frog, *Oophaga pumilio* (McVey et al. 1981, Nowakowski et al. 2013) and *Allobates femoralis* (Pašukonis et al. 2013, 2014a, b). Territorial *A. femoralis* males returned after translocations at a success rate of more than 80% for translocation distances of up to 200 m and 30% from 400 m (Pašukonis et al. 2013). Furthermore, tracking experiments revealed that *A. femoralis* relies on being familiar with an area for homing, and barriers like rivers affect initial homeward orientation (Pašukonis et al. 2014b). Nowakowski et al. (2013) found that only 67% of translocated *O. pumilio* returned from 20 m (N = 30) and 57% from 30 m (N = 30), suggesting a smaller homing radius in this species. Contrary to most *Allobates* species, female *O. pumilio* deposit their tadpoles in phytothelms within or close to their established territories (Pröhl & Berke 2001). Differences in life history, such as smaller territories and shorter tadpole transport distances in the case of *O. pumilio*, might explain lower homing performance. However, different sampling methods vary in their recapture potential and may also produce different observed return rates. More comparative studies with standardised sampling methods are needed to understand if natural history traits determine the homing performance in dendrobatid frogs.

Allobates talamancae is a small dendrobatid frog common in Central America. Males defend territories in the leaf litter and transport tadpoles to aquatic deposition sites on the forest floor outside their territories (Summers 2000). If homing ability is related to spatial behaviour in this species, such as extraterritorial tadpole transport, we might find that high homing performance is characteristic of the genus *Allobates*. In this study, we quantify the homing success and speed of male *A. talamancae* after experimental translocations.

Allobates talamancae is a small dendrobatid frog (average 20.5 mm SVL cf. Cope 1875) from Central America. Males advertise and defend small territories (mean size 13.1 m², SD = 4.4 m²; Summers 2000). Mating and clutch deposition take place in the leaf litter in the male's territory throughout the year and peak during the rainy seasons (Savage 2002). Males transport 8–29 tadpoles on their back to small water bodies on the ground (Duellman & Trueb 1994, Summers 2000, Savage 2002). Females have also been observed carrying tadpoles (K. D. Wells pers. comm. in Summers 2000). Because suitable tadpole deposition sites are scarce, most males will have to travel outside their territories for tadpole transport (pers. obs.). Males mainly call during low-light periods, in the morning and late afternoon, perched on leaves or elevated structures like tree stumps and branches. Calling usually peaks in the afternoon after rain (Savage 2002). Males start calling or show a phonotactic response towards a playback of an advertisement call of a simulated territorial intruder (Lechelt et al. 2014). The sexes are distinguishable in the field by their colour patterns: males have a dark coloured throat and chest, whereas females and juveniles have a white throat and belly (Summers 2000, Savage 2002). All frogs encountered in the area were caught, photographed and identified by their unique lateral coloration patterns.

The study area encompassed a fallow cacao plantation within secondary lowland rainforest adjacent to the tropical field station La Gamba (8°42′03.7″ N, 83°12′06.1″ W) and the national park Piedras Blancas, Costa Rica. The selected plot was a flat area bordering a stream on one side and a steep slope on the other.

The present data were collected over two field experiment periods during the beginning of the rainy seasons in 2012 and 2013. In 2013, we detected and captured 35 calling territorial frogs in our study area. Capture locations were recorded with a GPS device (MobileMapper™ 6, Spectra-Precision, Westminster, CO, USA) using the mobile GIS software ArcPad™ 10.0 (ESRI, Redlands, CA, USA) and marked with flagging tape. To confirm male territoriality, we attempted to recapture each individual at the marked initial capture sites within the next few days. Long-distance (200 m) translocations were carried out from 2–31 August 2013. Territorial males were captured in an airtight plastic bag, placed in an opaque container, and rotated multiple times for disorientation. Two groups of five individuals each were translocated 200 m away from their territories into two different directions. One group was released along the stream bordering the study area, the other one up the hill and away from the stream. Translocations were carried out on 3 and 4 August 2013. The release sites were marked and recorded on a GPS device. To quantify the recapture potential without translocation, we also rotated and released eleven territorial males without translocation (0 m control group). Additionally, after the recapture potential of the control group was quantified, five males from this group were translocated across the stream (40 to 70 m away from their territories) to test if streams constituted an obstacle for homing. The closely related *A. femoralis* typically avoids crossing running water and will make detours to find a terrestrial crossing point even across narrow and shallow streams (A. Pašukonis unpubl. data). The stream in our experimental area was three to five metres wide and did not provide any terrestrial crossing opportunities.

To quantify the homing ability of translocated frogs and the recapture success for the control group, we attempted to recapture both the translocated and control males back at their territory. The territories of all manipulated frogs were checked at least three times a day for 7 to 8 days or until recapture. To increase the chances of detecting these males, we briefly played a recording of a male advertisement call close to the supposed territories, simulating a territorial intruder. Every detected frog was captured and its individual lateral colour pattern compared to our catalogue of digital images. Sampling was paused from 12–17 August and afterwards resumed and continued until 31 August 2013 by checking the territories once a day between 9:30 and 10:00 h.

Data for short-distance translocations (20 m) were obtained from a previous study by L. Kopeinig (unpubl. data). Her observations had been made from 21 July through 16 August 2012. No GPS data were recorded. Twelve frogs were translocated to 20 m, then four of them to 50 m, and one of them to 100 m. However, there were some important differences in the experimental design between the two datasets. In 2012, the same individuals were repeatedly translocated in each cardinal direction for each distance starting from 20 m towards West. Only the frogs that returned four times from 20 m (once from each cardinal direction) were subsequently translocated to 50 m and so forth. Individuals were not rotated before translocation. For maximum comparability, only the data from the first translocation to 20 m for each individual was compared with our dataset from 2013. These twelve individuals were translocated on different days between 12 July and 7 August 2012. Like in 2013, the territories of all translocated frogs were acoustically and visually inspected at least three times a day until 16 August.

Frogs recaptured after the sampling break were considered outliers (3 individuals), because their return time estimates were not accurate. We included them in the analysis, but results are displayed including and excluding the frogs recaptured after the regular sampling period of 10 days to point out the difference. Wilcoxon rank sum tests and Fisher's exact tests were performed in "R" (R Development Core Team, 2008).

Seventy-seven percent of the translocated frogs were recaptured in their home territories within 21 days after translocation (Table 1). Nine of eleven control frogs were recaptured, and all of these were recorded inside their home territories within a maximum of seven days. Seven out of ten frogs translocated over 200 m were recaptured in their home territories. Out of these, three had returned from the hillside and four from along the stream. Ten out of twelve frogs translocated for 20 m were recaptured in their territories.

Table 1. Summary statistics for recapture times (days) of translocated territorial *Allobates talamancae*.

Translocation distance	N	Mean	Median	SD	Min	Max	Range
0 m (control)	9	4	3	1.94	2	7	5
20 m	10	4.1	3	3.31	1	12	11
200 m	4	5	5.5	1.41	3	6	3
200 m (with outliers)	7	11.1	6	7.82	3	21	18
Total	26	5.87	4.5	5.11	1	21	20

Return times for the 200-m translocated frogs varied from 3 to 21 d ($\bar{x}$ = 11.14, SD = 7.82). Control frogs were recaptured within 7 d ($\bar{x}$ = 4, SD = 1.9). Return times for 20-m translocated frogs varied from 1 to 12 d ($\bar{x}$ = 4.1, SD = 3.3) (Table 1 and Fig. 1). There was no detectable difference between recapture times of the control group and frogs translocated for 20 m (Wilcoxon rank sum test: W = 47.5, p = 0.87). There was also no statistically significant difference between recapture times between 20 and 200 m (p = 0.093), but our sample size may be too small for comparison.

The recapture success was similar for all groups (Table 2). We recaptured 81.8% of control frogs and the total homing success was 77.3%. There was no detectable difference between recapture success of the control group and either of the translocated frog groups (Fisher's exact test: p = 0.76). Out of five frogs translocated across the stream, one returned during our sampling period. Overall, we recaptured frogs from all three directions that were included in the experiment.

Our results show a high homing performance in *A. talamancae* males translocated to 20 m and 200 m from their territories. Taken together with similar findings in *A. femoralis*, they suggest that high homing performance is possibly characteristic of the genus *Allobates*. There was no significant difference between the recapture times of the control group and frogs translocated for 20 m, suggesting that frogs returned as fast as we could possibly detect given our overall recapture effort. Furthermore, the mean return time did not vary substantially between these translocation distances; however, there was much greater variation in the return time from more distant release spots. Finally, one translocated frog returned from across the stream, demonstrating the ability to overcome such obstacles.

The recapture success of the control group (81.8%) was comparable to the homing success of the translocated frogs (77.3%), indicating that more individuals might have returned but were not detected. Furthermore, the similarity to the recapture rate of control frogs demonstrates that they returned at the highest rate we could detect with our sampling methods. Alternatively, some non-territorial males might have been included in our sample or shifted their territories during the sampling period. The overall homing success we have observed is comparable to that found in a larger dendrobatid frog, *A. femoralis* (Pašukonis et al.

Table 2. Male *Allobates talamancae* homing success after experimental translocation.

Translocation distance	N	Homing success (% recaptured)
0 m (control)	11	81.82
20 m	12	83.32
200 m	10	70.00
Total (20 m and 200 m)	22	77.27

2013). The smaller body size of *A. talamancae* (mean SVL *A. talamancae* = 20.5 mm cf. Cope 1875; mean SVL *A. femoralis* = 26.8 mm cf. Roithmair 1992) does not appear to be a limiting factor for its long-distance homing ability. Interestingly, the recapture potential of the control group was lower in *A. talamancae* (81.8% recaptured, mean recapture time 4 days) than in *A. femoralis* (100% recapture, mean recapture time 1.4 days) even though *A. femoralis* territories were sampled only once a day. This difference might reflect a higher site fidelity and stronger territoriality in *A. femoralis*, especially as territorial males were usually detected with the help of a stimulating playback. We may have failed to detect the presence of males because they did not respond to the playback. Because male territories are rather unstable in the beginning of the breeding season, it is also possible that we would have observed stronger territoriality if we had conducted the study later in the breeding season. Since males returned from 200 m almost as successfully as from 20 m, the maximum homing distance for *A. talamancae* remains unknown. Homing success of *A. femoralis* males decreases significantly from distances > 200 m (Pašukonis et al. 2013), which corresponds to the maximum tadpole transport distances in this species (185 m cf. Ringler et al. 2013). Tadpole transport distances for *A. talamancae*, as for most other dendrobatid frogs, remain unknown.
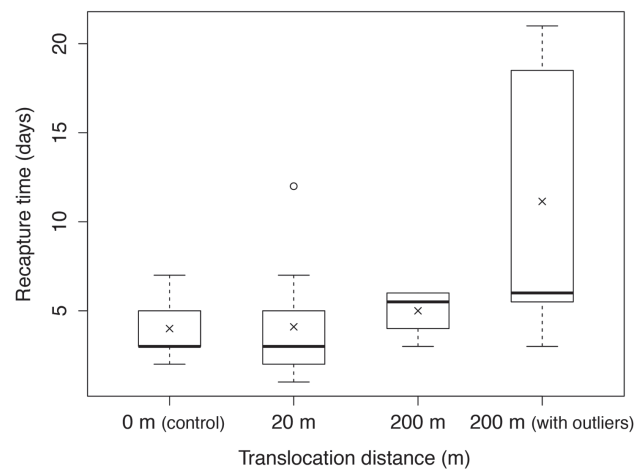

Figure 1. Recapture times in days of frogs translocated for 0 (control), 20, and 200 m from their territories. Results for 200 m are shown excluding and including three outlier points (17, 20, and 21 days). Black boxplot bars indicate the median and x-symbols the mean.

There was also high variation in recapture times between individuals translocated over the same distance with a large overlap in recapture times between the two distances. Some individuals took as long as 11 days to return from 20 m while others returned from 200 m within 3 days. Similar findings were reported for *A. femoralis* (Pašukonis et al. 2014a). Tracking experiments in *A. femoralis* showed that homing consisted of up to several days of immobility and shorter periods of rapid movement (Pašukonis et al. 2014a). Translocation experiments with *A. femoralis* were conducted over longer periods and part of the variation could be explained by changing weather conditions. In our study, weather conditions cannot account for the return time variation observed between individuals translocated for 200 m. We conducted all 200-m translocations within two days so that the translocated frogs experienced similar weather conditions during homing. Our results indicate individual differences in homing behaviour. The high variation in return times could be due to different physical conditions, experience, and motivational states of individuals. Less fit individuals might travel at a slower pace and pause more often for foraging. In addition, males having clutches to attend should be more motivated and move faster. If *A. talamancae* rely on familiarity with the environment for orientation, individually different degrees of this familiarity with a given area might also explain the variation in return times. Furthermore, terrain structure and the chosen route could affect return time and ability. While difficult terrain (e.g., steep relief, rocky areas, fallen trees) could increase the time needed for traversing an area, spots that fit a male's territorial needs better could also interrupt or even stop homing behaviour in favour of resettlement.

A recent study revealed that *A. femoralis* relies on its familiarity with an area for successful homing (Pašukonis et al. 2014a). Movements during tadpole transport or juvenile dispersal could lead to a memorised spatial map that is used for orientation. In other amphibian species, translocation experiments also suggest that familiarity with an area affects homing ability (reviewed in Sinsch 2006). Tadpole transport potentially requires a good knowledge of where to find water bodies to carry offspring to. Our results suggest that high homing performance may be characteristic for the genus *Allobates*. This ability could be linked to regular tadpole-shuttling between home territories and extra-territorial deposition sites, which is common in this genus. More comparative translocation studies of dendrobatid frogs may reveal a link between such natural history traits and homing performance.

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