

Homing behavior in the Neotropical poison frog *Ameerega trivittata*

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Abstract. Neotropical poison frogs (Aromobatidae, Dendrobatidae) are known for their complex behavior including site fidelity and home range maintenance. It has been shown in a few poison frog species that these amphibians are able to return to their home ranges after experimental translocation. In this study we asked if *Ameerega trivittata* can be allocated to the species performing homing behavior. In this taxon, males and females show home range behavior, while sexes were not distinguished in our study. Fieldwork was carried out in a wild population at Panguana (Peru), using replacement distances of 150 m, 600 m and 900 m. In total, 79 frogs were translocated. Most rapidly returned to their home ranges from all translocation distances, with a decrease of the homing success with longer distance. Among the poison frogs studied so far, it is remarkable that *A. trivittata* is the only one known to be able to return from 900 m (which perhaps is a remarkable homing distance for anurans in general), while maximum return distances in other species are less than 50% of this. *Ameerega trivittata* is one of the largest poison frogs (maximum snout–vent length 55 mm). However, long distance homing was not explained by the species' body size. We rather expect that 'good knowledge' of the general area (in terms of integration of learned landmarks) that frogs live in is the reason for the ability of long distance homing in our focal taxon.

Key words. Amphibia, Anura, Dendrobatidae, experimental translocation, Peru, site fidelity.

Introduction

Homing behavior in animals is defined as the ability of an individual to return over little or unknown terrain to the place where it 'lives', its home range (BURT 1943). This phenomenon was reviewed by PAPI (1992) and LAVAR & KELLY (2008) and is found in many arthropods and vertebrates, such as decapod crustaceans (PITTMAN & MCALPINE 2003), salmon (QUINN & DITTMAN 1990) or pigeons (WALCOTT 1996). Various advantages of such site fidelity have been discussed, in particular the maximization of resource exploitation, which often is related to reproduction.

Among the Amphibia, many species are known to show site fidelity (SINSCH 2014). This is frequently accompanied by seasonal migratory return, such as to a 'traditional' breeding pond (DUELLMAN & TRUEB 1986, SINSCH 2006, 2014, WELLS 2007). As a result of this, numerous amphibians are able to perform homing behavior; what can be studied through experimental translocation (reviewed by SINSCH 1990). As summarized by WELLS (2007), homing behavior in salamanders and newts is relatively well understood, compared to other amphibians. In frogs and toads, homing behavior so far has mostly focused on nocturnal taxa from the temperate region (e.g., BOGERT & STATION 1947, DOLE 1968, JAMESON 1957, TWITTY et al. 1964,

HOLENWEG PETER et al. 2001). In recent years, there has been some research progress with regard to diurnal terrestrial anurans from the Neotropics, mainly in the intriguing group of poison frogs of the families Aromobatidae and Dendrobatidae (NOWAKOWSKI et al. 2013, PAŠUKONIS et al. 2013, PICHLER et al. 2017).

Poison frogs are a diverse group of small (ca. 2–6 cm adult size), almost exclusively diurnal amphibians, associated with humid habitats from rain forest to páramo (GRANT et al. 2006). They are well known for having bright vivid colorations and skin toxins, although about two thirds of the ca. 300 taxa lack these traits (cf. KAHN et al. 2016). Poison frogs show complex reproductive and social behaviors, including larval transport by parent frogs to small water bodies and other parental brood care strategies, intraspecific aggressiveness and complex interspecific mimicry (LÖTTERS et al. 2007). Many species show strong site fidelity and defend territories in one or both sexes (PRÖHL 2005). This behavior is suggested to be associated with the utilization of beneficial resources, such as food or shelter availability, or to be profitable in mate attraction. Resource use also explains homing behavior observed in some poison frog species (NOWAKOWSKI et al. 2013, PAŠUKONIS et al. 2013). An additional reason for pronounced homing abilities is that water bodies utilized for larval deposition are of-

Table 1. Summary of homing behavior in poison frog species after experimental translocation.

Species, sex, country	Translocation distance	Successful homing rate	Source
Aromobatidae			
<i>Allobates femoralis</i> , males, French Guiana (SVL ≤ 33.5 mm)	50 m	80% (N = 10)	PAŠUKONIS et al. (2013)
	100 m	100% (N = 10)	
	200 m	80% (N = 10)	
	400 m	30% (N = 10)	
	800 m	0% (N = 10)	
<i>Allobates talamancae</i> , males, Costa Rica (SVL ≤ 24.0 mm)	20 m	83.32% (N = 12)	PICHLER et al. (2017)
	200 m	70% (N = 10)	
Dendrobatidae			
<i>Oophaga pumilio</i> , males and females, Costa Rica (SVL ≤ 24.0 mm)	3 m (females only)	80% (N = 5)	MCVEY et al. (1981)
	6 m	90% (N = 10)	
	12 m	90.91% (N = 11)	
	20 m (females only)	83.33% (N = 6)	
<i>O. pumilio</i> , sexes not distinguished, Costa Rica	20 m	67% (N = 30)	NOWAKOWSKI et al. (2013)
	30 m	57% (N = 30)	

ten limited and specimens have to carry tadpoles over several hundred meters away from their home ranges (PRÖHL & HÖDL 1999, RINGLER et al. 2009). As summarized in Table 1, of the 18 genera in the two poison frog families, homing after experimental translocation has been examined in three species of two genera only (MCVEY et al. 1981, NOWAKOWSKI et al. 2013, PAŠUKONIS et al. 2013, PICHLER et al. 2017). All of them displayed a clear tendency to return, but return rates decreased with distance. In this paper, we study homing behavior in a species of the dendrobatid genus *Ameerega*.

Ameerega trivittata (SPIX, 1824) is a day-active, wide-spread Amazonian lowland taxon (SILVERSTONE 1976). Both sexes in this comparatively large poison frog (maximum size 55 mm) perform home range behavior and males are suggested to defend part of their home ranges as territories (ROITHMAIR 1994, LUIZ et al. 2015). Home ranges are highly variable in size and can be remarkably large. According to NEU et al. (2016), the average home range size in males and females is $420.08 \pm 148.02 \text{ m}^2$ and $524.48 \pm 87.56 \text{ m}^2$, respectively. Site fidelity in males is suggested to be related to the presence of resources that are advantageous to reproduction, such as exposed habitat structures (e.g., fallen trees) for emitting vocalizations with the goal to attract females (ROITHMAIR 1994, ACIOLO & NECKEL-OLIVEIRA 2014). The motivation for female site fidelity remains unknown (cf. NEU et al. 2016).

Because of the observed site fidelity in *A. trivittata* we expected this species to exhibit homing behavior (like other poison frogs). The goal of our study was to explore this in a wild population via experimental translocations. We hypothesize that (1) homing behavior of *A. trivittata* decrease with an increase of translocation distance. Given the species' large body size and home range size, we hypothesize that (2) *A. trivittata* individuals are able to return to

their home ranges over longer distances than the previously studied, smaller poison frog species. In concert with this, we hypothesized that (3) successful homing increases with larger body size among conspecifics of the study species.

Material and methods

Translocation experiments

Fieldwork was carried out between 25 February and 8 April 2015 at Panguana Biological Field Station, Region Huánuco, Peru. It is situated in the Amazon lowland rain forest on the lower Río Lullapichis ($9^{\circ}37' \text{ S}$, $74^{\circ}56' \text{ W}$, ca. 260 m above sea level), a tributary to the Río Pachitea (SCHLÜTER 2005). The population of *A. trivittata* in the surroundings of this field station was already investigated in previous life history studies (e.g., ROITHMAIR 1994, NEU et al. 2016).

A total of 91 individuals were collected for experimental displacement. All were caught after sunset (latest on 21 March) when sleeping on vegetation. Males and females of this species, if at all, only slightly differ in external morphology so that when collecting them the sexes are hard to tell apart. In this study we did not determine the sexes. For clarification, in another study on *A. trivittata* (NEU et al. 2016), we distinguished males and females, but this was done on day-long observations of calling and mating. Specimens had mean snout-to-vent length (SVL) $40.18 \pm 0.04 \text{ mm}$, ranging from 35.0 to 48.0 mm. Given these data, we considered all test individuals as adults (cf. ACIOLO & NECKEL-OLIVEIRA 2014, LÖTTERS et al. 2007). Digital photographs of the dorsal pattern of each frog were taken using a Fuji FinePix S2500HD digital camera. Photographic data were used for individual recognition from a distance of up to 3 m (cf. SILVERSTONE 1976). Captured individuals were singly placed in plastic containers with humid sub-

Table 2. Distance classes used in translocation experiments and the number of specimens of *Ameerega trivittata* randomly assigned to each cardinal direction.

Distance class	East	South	West	North	Total
150 m	6	8	9	8	31
600 m	9	13	3	7	32
900 m	4	5	3	4	16
Total	19	26	15	19	79

strate until they were released on the next morning before 09:00 h. Collection sites were marked with a plastic tag; the coordinates and elevation above sea level were taken with a Garmin eTrex 30 GPS receiver.

In total, 91 specimens were collected. By flipping a coin, we randomly decided if a specimen was translocated or released the other day at the exact collection sites. The latter was performed to examine the recapture potential without translocation (control group). In accordance with other field-based studies on poison frog homing behavior (e.g., PAŠUKONIS et al. 2013, PICHLER et al. 2017), for 79 frogs to be translocated, we used (each chosen using random numbers) three distance classes and all four cardinal directions for translocations (Table 2). The GPS receiver was used to determine distances and directions in the field; in addition, coordinates and information on elevation above sea level of capture and release points were GPS-recorded.

For indication of successful homing, subsequent to translocations or release at collection site (i.e., control group), always the same fieldworker searched for the individuals within the area of their collection sites at least every third day. We allowed a ca. 30 m radius around the original collection site, due the relatively large home ranges occupied by this species (cf. ROITHMAIR 1994, NEU et al. 2016). Due to the diurnal activity of *A. trivittata*, we mainly conducted searches for frogs during day time. Twenty-minute-searches were performed. For individuals that were retraced, this was 1–16 searches (4.34 ± 3.40 , $N = 41$); for those not found, this was 5–14 searches (9.70 ± 2.42 , $N = 50$).

Data analysis

In the field, it was difficult to translocate frogs at the exact distance. Thus, differences between intended distances (i.e., 150, 600 and 900 m) and the actual distances (m) between capture sites and release points (i.e., GPS marks) were determined with ArcGIS 10.3 (Esri®). Student's *t*-tests for paired samples (normally distributed data with homogeneity of variance was previously confirmed) was conducted to identify differences between the intended (i.e. exact) and the actual translocation distance in the field. Results revealed statistically significant differences for the 600 m and 900 m distance (150 m: $t = 1.563$, $df = 30$, $p = 0.1286$; 600 m: $t = 2.466$, $df = 30$, $p = 0.0194$; 900 m: $t = 2.561$,

$df = 15$, $p = 0.02174$). For further analyses, the actual distances (m) were used.

We calculated a Generalized Linear Model (GLM) with 'logit link' for data with binomial distribution, i.e., a logistic regression model. Homing of individuals was the binary response variable and translocation distance (m) and cardinal direction (ordinal data) of individuals, SVL (mm) and altitudinal difference between capture and release place (m) were considered as potential predictor variables. The global model was simplified using stepwise AIC (Akaike Information Criterion) selection and model fit was obtained by calculating the area under the receiver operating characteristic curve (AUC) of the best fitting model. AUC values range from 0.5 to 1.0 whereas values > 0.7 describe "usable", > 0.8 "good" and ≥ 0.9 "very good" models (SWETS 1988).

With the goal to identify effects of the three different group size of distance classes and the control group, a FISHER's exact test was conducted. We tested for significant differences between the numbers of days after which frogs were recaptured among the three distance classes via a chi-square test.

All statistical analyses were performed in R (R Development Core Team 2008: "R: a language and environment for statistical computing"; <http://www.rproject.org>), using the packages *mass* and *verification*.

Results

Homing behavior in *A. trivittata* was found for all three distance classes. Thirty-four of the 79 translocated individuals (i.e. 43%) were recaptured within the area of their original collection sites, i.e., their assumed home ranges (Table 3). Seven of the 12 control group frogs (i.e. 58%) were retraced at their capture sites. There was neither a statistically significant difference in homing success between the distance classes, nor between each of them and the control group (FISHER's exact test: $p > 0.05$). However, an exception from this was noted between the 150 m and 600 m distance classes (FISHER's exact test: $p = 0.014$). The time period after which frogs had returned varied markedly (Table 3) and there was no significant difference among these time periods (chi-square test: $p > 0.05$).

The best fitting model (with $AUC = 0.7$) only included the translocation distance of the individuals as predictor variable. Translocation distance negatively affected *A. trivittata* homing behavior ($Z = -3.72$, $P < 0.001$), while the other considered variables had no effect on it. Already at about 400 m translocation distance, the predicted homing of individuals was 50% only (Fig. 1).

Discussion

Successful homing behavior

Like other poison frog species (Table 1), *A. trivittata* displays site fidelity (cf. ROITHMAIR 1994, NEU et al. 2016).

Table 3. Information on successful homing behavior *Ameerega trivittata* for three distance classes studied plus a control group (cf. Table 2).

Distance class	Number of specimens (with percentage of each all translocated specimens)	Mean period after which specimens were recaptured (with range in parentheses)
150 m	23 (74.19%)	9.09 ± 1.7 (2–30) days
600 m	7 (21.88%)	14.14 ± 2.38 (5–21) days
900 m	4 (25.00%)	13.63 ± 1.44 (11–17) days
total	34 (43,04%)	12.29 ± 1.61 (2–30) days
0 m (control group)	7 (58.33%)	6.57 ± 1.49 (2–14) days

As hypothesized by us, our results clearly indicate that this species performs homing behavior after experimental translocation, decreasing with translocation distance. In fact, homing success was explained in our GLM by translocation distance. Comparing observed return rates to those in other aromobatid and dendrobatid species (Table 1; Fig. 1), *A. trivittata* behaved largely similar to them. However, as already pointed out by PICHLER et al. (2017), comparisons are generally hampered due to the absence of standardized methods.

Actually, we expect that true returns in our study were even higher than determined and that we had overlooked some frogs. Reasons for this include: (i) the probability of detection/redetection of individuals remains an imperfect issue (cf. HOLENWEIG PETER et al. 2001, SCHMIDT 2003; WAGNER et al. 2011); (ii) home ranges in *A. trivittata* can be considerably large (ROITHMAIR 1994, LUIZ et al. 2015, NEU et al. 2016) so that *a priori* retracing specimens remains a hard undertaking; (iii) the searches for specimens that we considered as ‘not retraced’ was (for logistical reasons) not standardized, leaving the possibility that actually

more than the 41 *A. trivittata* individuals had returned to their home ranges.

Remarkable is the relatively low number of recaptured specimens that were not displaced (i.e., the control group), especially when compared to other poison frog homing behavior studies (e.g., PAŠUKONIS et al. 2013, PICHLER et al. 2017). It appears unlikely to us that all untraced individuals had disappeared from their home ranges in response to collecting them. On other occasions, we often collected and handled *A. trivittata* individuals and they seemed unaffected by this (cf. NEU et al. 2016). We argue that rather we might have overlooked these frogs for other reasons such as again a low detection probability and the species’ large home size already mentioned.

Regarding the duration after which individuals could be retraced near their collection sites, i.e., after homing, varied greatly and did not depend on distance. This illustrates that even after displacement over long distances, *A. trivittata* is able to return rapidly. This is an observation shared by other aromobatid and dendrobatid species (MCVEY et al. 1981, NOWAKOWSKI et al. 2013, PAŠUKONIS et al. 2013, PICHLER

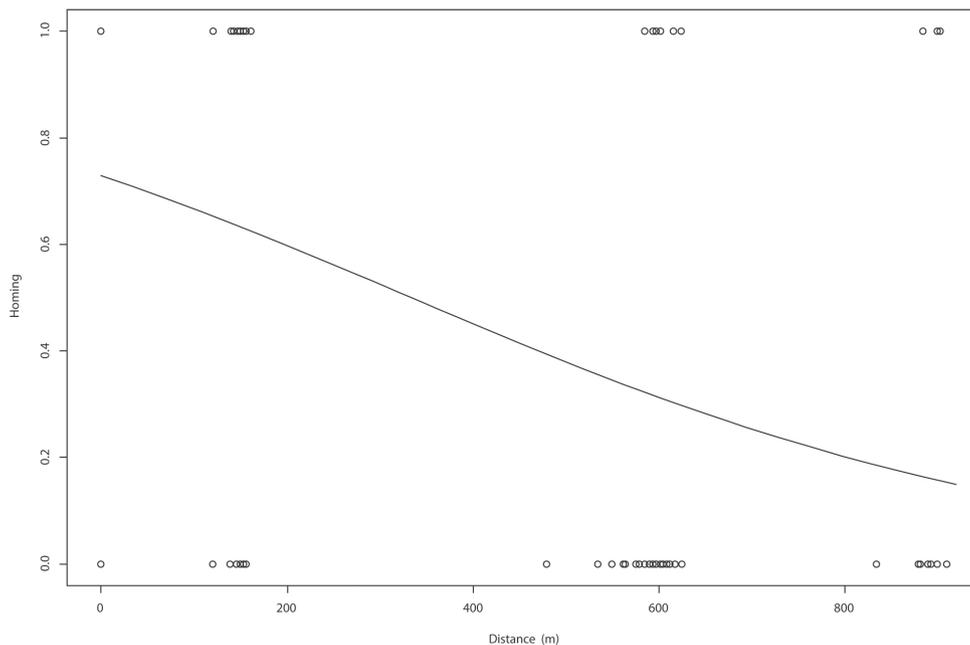


Figure 1. Predicted homing success of *Ameerega trivittata* individuals translocated at different distance classes (0, 150, 600, 900 m).

et al. 2017). While this certifies a highly developed sense of orientation, the navigation mechanisms in poison frogs remain unknown, as in general amphibians can make use of various modes (compass orientation, beaconing, pilotage, path integration, true navigation; SINSCH 1990, 2006). *Allobates femoralis*, after experimental displacement and radio-tracking, moved straight paths to their home ranges (PAŠUKONIS et al. 2014 a, b). The authors suggested that spatial learning and orientation on landmarks could be the orientation mechanism in this poison frog species. Such landmarks remain unknown but could be represented by fallen trees, water bodies etc. *Ameerega trivittata* homing behavior in our study was neither influenced by altitudinal differences between collection site versus release point nor by cardinal direction, perhaps suggesting that frogs in general know the terrain and use landmarks for orientation.

As with regard to poison frogs in general, beside arobatids, not only dendrobatids in the genus *Oophaga* but also in the distantly related (cf. GRANT et al. 2006) genus *Ameerega* are able to conduct homing.

Homing over long distance and the role of body size

One of our hypotheses was that *A. trivittata* is able to return over longer distances than the four other poison frog species that have been studied so far. Our data demonstrate that *A. trivittata* specimens are able to find back to their home ranges after displacement for up to 900 m. Such a

large distance has not been examined yet in any other poison frog taxon – and its confirmation might generally be considered remarkable in small- to mid-size anurans (cf. HOLENWEIG PETER et al. 2001). Return rates in *Allobates talamancae* and *Oophaga pumilio* (MCVEY et al. 1981, NOWAKOWSKI et al. 2013, PICHLER et al. 2017) suggest that certainly these frogs are unable to find back to their home ranges when displaced for such a large distance (Fig. 2). Only in *Allobates femoralis*, frogs were experimentally displaced for 800 m – but none returned (PAŠUKONIS et al. 2013). Thus, our hypothesis is corroborated.

One rationale for our hypothesis was that *Ameerega trivittata* is considerably larger than the other studied species (cf. Table 1). For instance, *Allobates femoralis*, the largest of them, has only about two thirds of the SVL of *A. trivittata* (SILVERSTONE 1976, LÖTTERS et al. 2007). As body size might be related to interspecific differences, we hypothesized in addition that SVL among the replaced *A. trivittata* specimens had an effect on homing success, i.e., successful homing increased with larger body size. However, SVL was negated in our GLM as a potential predictor variable with regard to translocation distance class, so that our hypothesis has to be rejected. Also, PICHLER et al. (2017) proposed that differences in body size between *Allobates femoralis* and *A. talamancae* did not have an effect on homing performance.

As another reason, we assumed that the large home ranges recorded in our target species could explain long distance homing behavior. Although, we have not tested

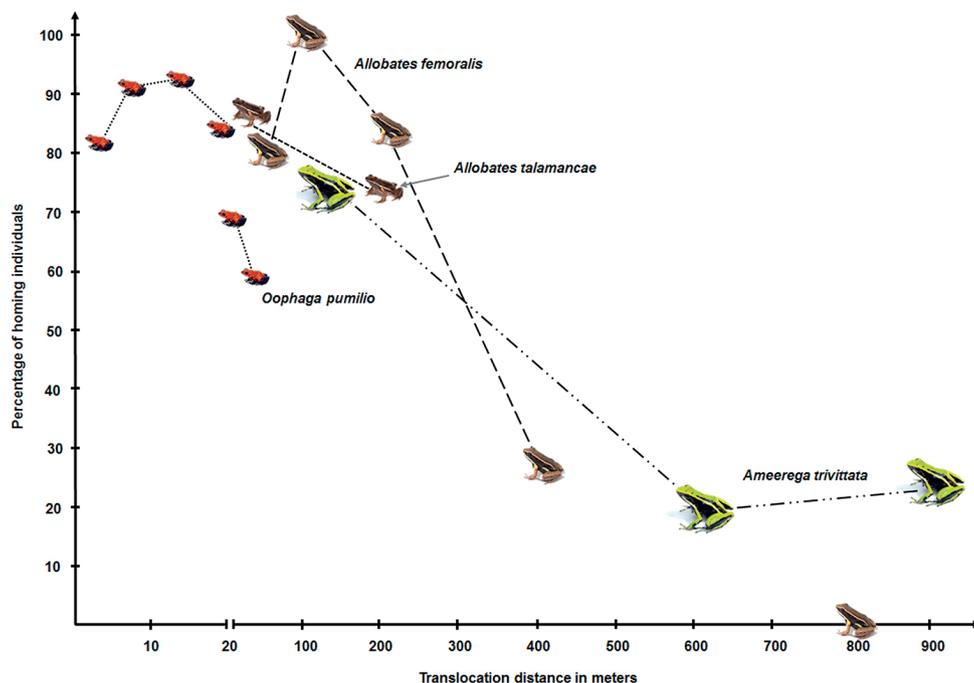


Figure 2. Successful homing in four poison frog species after experimental translocation (based on data in Tables 1 and 3). Size of iconized frogs is smaller than natural size but proportions to each other resembles natural conditions. Note that one species was translocated for 800 m with return rate zero. Photographs used are available via the worldwide web and were taken by B. WILSON, B. GRATWICKE, J. P. LAWRENCE, Rana Verde.

this further, there might be some rationale behind this. Poison frogs are suggested to have 'good knowledge' about the general area they live in by integration of learned landmarks (see above). In many species, this spatial learning is especially essential, as in many species, tadpoles are carried to water bodies which can be fairly distant from the place of terrestrial egg deposition (PRÖHL 2005, RINGLER et al. 2013, PAŠUKONIS et al. 2014a). This was confirmed for *A. trivittata* in which home ranges often do not contain water bodies suitable for larval development (ROITHMAIR 1994, LUIZ et al. 2015). This might promote frogs' orientation in geographic space. In this context, PAŠUKONIS et al. (2013) suggested that in *A. femoralis*, the decrease in homing performance was correlated with the maximum tadpole transport distance. In the majority of poison frogs, larvae are carried by males only – including *A. trivittata* (SCHLÜTER 2005, LÖTTERS et al. 2007). In this species, it is suggested further that males do not carry all tadpoles from one clutch at once (ROITHMAIR 1994, ACIOLO & NECKEL-OLIVEIRA 2014), which poses another strong argument that males are reliable homers. Altogether these are good arguments for male homing over long distances in our focal species.

In our study on *A. trivittata*, sexes could not be distinguished. In concert with the concept of 'good knowledge' due to repeated larval transport, we will not rule out that *A. trivittata* specimens performing long-distance homing in our study exclusively were males. On the other hand, females are less well studied and even the motivation for them to maintain home ranges remains unknown. This illustrates a noteworthy research deficiency, especially since females possess home ranges equal in size to those of males (NEU et al. 2016). In the case of *O. pumilio* it has been demonstrated that both sexes show solid homing behavior (MCVEY et al. 1981). In this dendrobatid, the female is strongly involved in brood care (i.e., the contrary to *A. trivittata*; ACIOLO & NECKEL-OLIVEIRA 2014). *Oophaga pumilio* males might perform homing as calling sites for mate attraction are beneficial, which is likewise not applicable to *A. trivittata* females. In addition, STAUDT et al. (2010) indicated that in *O. pumilio* food density (formicine ants) was higher in home range core areas than outside. It remains to be studied if this is a motivation for homing in poison frogs.

Conclusions and outlook

We have shown that *A. trivittata* is an additional poison frog that performs homing behavior and that this species is able to return from 900 m after experimental translocation. This is a remarkably long distance, not only for the group of Neotropical poison frogs but small- to mid-sized anurans in general. While the relatively large SVL of the study species may play a role for long distance homing, within-species variation of SVL did not explain homing success. It remains to be studied if home range size or sex play a role in *A. trivittata* homing behavior. Also, it might

be interesting to repeat this study with more standardized numbers of individuals per translocation class and perhaps even longer translocation distances. In this way, it can also be assessed if homing success decreases gradually, which cannot be stated with certainty from our results (Fig. 2).

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