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Seasonal overland dispersal of the Suriname Toad, *Pipa pipa* (Linnaeus, 1758), in the Peruvian Amazon

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Abstract. The Suriname Toad (*Pipa pipa*) is a highly aquatic species with cryptic habits, making field observations rare. Despite its presumed dependence on permanent waterbodies, overland dispersal of the species occurs but remains poorly understood. We investigated *P. pipa* movement patterns at an oxbow lake in the Peruvian Amazon using pitfall traps deployed in November 2012 (early wet season) and April 2013 (late wet season). A total of 18 captures indicated directional movement between permanent water and seasonal wetlands. Nine individuals migrated from permanent water to seasonally flooded areas as they became inundated, then returned to permanent water as these wetlands dried. Pitfall traps facing opposing directions caught no individuals, confirming movement directionality. This represents the largest number of *P. pipa* encounters documented at a single site, providing evidence for regular terrestrial activity in this species. Our findings suggest that seasonal hydrological changes drive overland dispersal, exhibiting patterns consistent with amphibian migration. We highlight the utility of pitfall trapping for studying *P. pipa* populations and provide a foundation for future studies on its dispersal ecology.

Keywords. Amphibian, Suriname Toad, dispersal, population, *Pipa*, pitfall trapping.

Introduction

The Suriname toad (*Pipa pipa*) is a highly aquatic species, with its biology closely tied to water availability (Cannatella and Trueb, 1988; Rodriguez and Duellman, 1994). Its cryptic habits and predominantly aquatic lifestyle make field observations rare, though previous studies indicate that it inhabits both permanent and ephemeral swamps (Buchacher, 1993; Rodriguez and Duellman, 1994; Duellman, 2005). However, most knowledge about *P. pipa* comes from captive studies (Rabb and Snedigar, 1960; Zippel, 2006; Alves-Pinto et al., 2014) while wild populations, particularly regarding movement and habitat use, remain understudied.

Pipa pipa exhibits one of the most unusual reproductive modes among anurans. During amplexus, the male fertilizes eggs as they are released, and repeated vertical somersaults in the water lead to the eggs becoming embedded in the female's dorsal skin (Rabb and Rabb, 1960). The skin swells around each egg to form "pores", individual dermal chambers where embryos develop completely and bypass a free-swimming tadpole stage (Rabb and Snedigar, 1960; Sokol, 1977). After 12–20 weeks, fully metamorphosed juveniles emerge from these chambers (Rabb and Rabb, 1963). Following emergence, the pores gradually heal, though they may remain visible as scars that provide evidence of past reproductive events (Cannatella and Trueb, 1986). Because breeding activity is directly linked to the availability of suitable aquatic habitats in this species, movement between waterbodies is potentially crucial to the species' ecology. In the congener *Pipa arrabali*, the use of multiple aquatic habitats and its ability to disperse freely across the landscape are well-documented (Gascon, 1992; Buchacher, 1993; Garda et al., 2006), suggesting that similar movement behaviours may exist in *P. pipa*.

Pantoja and de Fraga (2012) documented *P. pipa* captures in pitfall traps and provided direct evidence of overland dispersal between aquatic habitats. However, classifying such movement remains challenging, particularly when it involves mature individuals traveling long distances from suitable water sources (Semlitsch, 2008). While the presence of *P. pipa* in multiple aquatic

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environments suggests regular overland dispersal, no published studies have distinguished between random dispersal, in which individuals move opportunistically to colonize new habitats, and directional migration, in which movement is driven by breeding or seasonal environmental changes (Semlitsch, 2008). In tropical systems with pronounced wet and dry seasons, aquatic-breeding amphibians may exhibit movements associated with breeding habitat availability. During wet seasons, when ephemeral waterbodies become available, individuals can undertake breeding migrations from terrestrial refugia to aquatic sites (e.g., Tocher et al., 2001). Conversely, dry season movements may involve dispersal from drying habitats to more permanent waterbodies or terrestrial retreat sites (Buchacher, 1993; Abe, 1995). These directional seasonal movements contrast with opportunistic dispersal, where individuals move serendipitously to colonize newly available habitats regardless of season or reproductive status (Navas et al., 2016).

In the Amazon movement of *P. pipa* is likely tied to rainfall and seasonal flooding (Kahn and Mejia, 1990; Sombroek, 2001; Salovaara et al., 2005). Heavy rains create aquatic habitats when poor drainage in soils and interconnected waterbodies leads to flooding (Goulding et al., 2003; Moraes et al., 2021). This includes both permanently flooded swamps and forests, as well as seasonally flooded areas where excess water drains over a period of months (Junk et al., 2010).

Pitfall trap studies of pond-breeding salamanders have successfully quantified terrestrial movements between breeding and non-breeding habitats and provided key insights into population dynamics (Bailey et al., 2004; Gamble et al., 2007). These studies demonstrate the importance of linking wetland characteristics, such as surface area, shoreline length, and depth, to movement patterns. To achieve a similar level of quantification for *P. pipa*, integrating wetland measurements with trapping data is essential (Kinkead and Otis, 2007). Here, we document the dispersal of *P. pipa* based on long-term herpetofaunal monitoring in southwestern Amazonia and highlight the effectiveness of pitfall trapping in studying this highly elusive species.

Materials and Methods

Study area. The Amazon Research and Conservation Center (ARCC) is located along the Río Las Piedras in the Madre de Dios Region of southeastern Peru (12.0455°S, 69.67633°W; Fig. 1A). The concessions adjacent to the research station are managed by a conservation organization called Junglekeepers Peru and features an oxbow lake (Lago Soledad), which remains connected to its parent river via a small stream. The surrounding forest experiences annual inundation, with floodwaters extending 1–1.5 km inland during peak wet seasons. Seasonal flooding in Amazonian floodplains is primarily driven by rainfall in the wet season late in the year (December–March; Kahn and Mejia, 1990; Hill, 1999; Sombroek, 2001; Salovaara et al., 2005). On the Las Piedras River during the wet season these floodplains provide extensive aquatic habitat for a range of organisms, including fish, turtles, caimans, mammals, and frogs (Carvalho et al., 2012; Payne et al., 2024; Crnobrna et al., 2025). As water levels recede, Amazon floodplains undergo an extended dry period during the middle of the year, which drastically alters habitat availability (Goulding et al., 2003; Moraes et al., 2021).

Pitfall trap sampling. We installed eight pitfall trap arrays at ARCC between October and November 2012, maintaining them through mid-2013 for a total of 206 trap-nights. For this specific study, two traps (hereafter called Suriname Trap and Skyfall Trap; Fig. 1A) captured individuals of *Pipa pipa* over the course of 67 trap-nights. The Suriname Trap operated for 24 trap-nights from 5 November–1 December 2012, while the Skyfall Trap was deployed for a longer duration of 43 trap-nights, from 24 April–31 May 2013. Traps were placed at opportunistic locations 200, 500, and 600 m from the base lodge to facilitate daily checks as part of a long-term herpetofaunal monitoring program. Surveys at ARCC included transects, quadrats, acoustic monitoring, artificial breeding habitats, and opportunistic searches, the latter targeting areas not covered by regular monitoring, such as a second oxbow lake and small swamps. Although 96 h of opportunistic search time were recorded, comprehensive documentation of all flooded areas was challenging. To address this, we marked five representative points (crosses in Fig. 1A) to identify standing water and flooded forest physiognomy, characterized by soil mounding on hummocks associated with palms and trees (e.g., genera *Attalea*, *Ficus*, *Mauritia*, and *Oenocarpus*). The hollow areas between these mounds fill with water during high-water seasons and they play a significant role in shaping the region's floodplain microtopography (Kahn and Mejia, 1990; Hill, 1999; Salovaara et al., 2005).

For pitfall trap construction, we used plastic sheeting trenched into the ground and secured to 70 cm height by driving sticks through the plastic. We used additional soil taken from the holes dug for the buckets to backfill

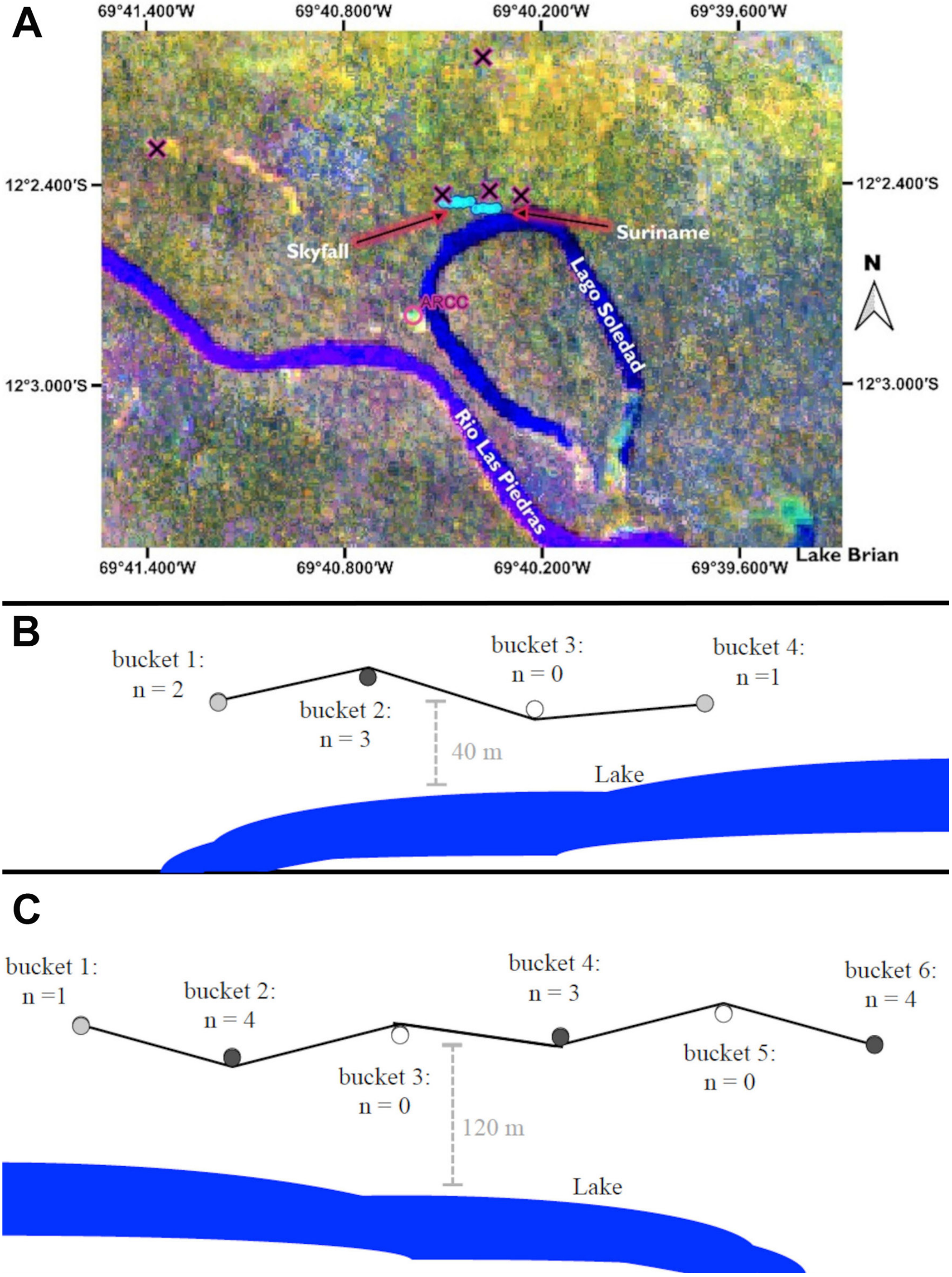

Figure 1. Sampling arrangement of *Pipa pipa* in Las Piedras, Peru. (A) Site map and false-colour composite of Sentinel-2A satellite imagery (SEPAL; FAO, 2020) depicting the study area. Darker forested regions represent non-flooded forest, while lighter yellow regions indicate swamp habitats. Flooded forest ground-truthing points (crosses) are positioned along the margins of these swamp areas. The offsite oxbow lake, where opportunistic *P. pipa* encounters occurred, is visible in the bottom right corner. The composite is based on 27 December 2017 providing a wet-season representation. (B) Suriname Trap (November–December 2012, wet season). (C) Skyfall Trap (April–May 2013, dry season). The diagrams in (B) and (C) illustrate the placement of pitfall buckets (circles), with black-filled circles indicating captures of *P. pipa* (n = number of captures, < 3 captures filled grey). The dashed vertical lines denote the distance from the lake shoreline. The absence of captures in specific buckets shown in white highlights the directional movement of *P. pipa*, supporting seasonal migration between permanent and temporary waterbodies.

along the drift line to prevent frogs passing under the fence. We laid out the drift fences in straight lines in an attempt to intercept animals moving between habitats. We constructed pitfalls with four 20-l plastic buckets spaced 10 m apart, to complete a 30-m drift fence. We situated the middle two buckets (Buckets 2 and 3) to exclude one side of the barrier, thus allowing the tallied captures to each represent a single, exclusive probability of capture (outcome of a trial). However, we ran the drift fence over the centre of Buckets 1 and 4 to sample animals encountering the fence from either side of the barrier, and distributing the probability assigned to captures equally to 0.5 per capture. Bucket 2 was oriented to sample upland habitat, while Bucket 3 faced the lake (Fig. 1B).

We modified this design for the expanded pitfall program at the Skyfall Trap, which had a greater number of buckets and therefore a longer drift line. In this trap, two 20-l buckets sampled inland habitats, alternating with two 20-l buckets facing the lake, which allowed us to replicate the probability distributions. In contrast to the Suriname Trap (40 m from the lake), we placed the Skyfall Trap further inland from the lake (120 m; Fig. 1C). We used 60-l buckets for Buckets 1 and 6, so six buckets connected a 50-m drift line. Placed in the 500 m range from our base, the opportunistic position was closer to seasonally flooded forest but further away from the lake. However, we situated both traps with drift lines parallel to the lakeshore. We measured 478 m of lakeshore by directly walking the shore and storing a GPS track log (GPSmap 60csx, Garmin, Schaffhausen, Switzerland). For the remaining lakeshore, we plotted midpoints between track logs made with the GPS unit corresponding to mid-lake and lakeshore trails, generating trap line distance to water and total lakeshore figures.

We used rainfall data to characterise seasonal precipitation patterns and contextualize the timing of our sampling periods relative to wet season rainfall events, which allowed us to assess whether frog movements corresponded with seasonal hydrological conditions. We gathered rainfall data from the meteorological station in Puerto Maldonado, Madre De Dios Region, which belongs to the Peruvian Atmospheric and Meteorological Service (SENAMHI, 2018). This is the nearest available meteorological station (~ 80 km distant).

Pitfall trapping was conducted in phases lasting from several weeks to one month, with traps checked daily to ensure proper function and animal welfare. Investigators maintained the traps by covering buckets, removing non-target captures (e.g., spiders, ants, centipedes), and preventing infilling by leaf litter. Data were recorded for all amphibians, reptiles, and small mammals captured. During daily checks, we identified buckets with poor drainage. When rainfall caused water levels to exceed the drainage capacity of the perforated bucket bottoms, the risk of drowning for snakes, lizards, and other trapped animals increased. To mitigate this, we uninstalled traps under such conditions, which limited sampling duration. All specimens of *P. pipa* were released directly into Lago Soledad at sites over 250 m away from the traps. For reasons of taxonomic and biogeographic study, one specimen of *P. pipa* (field tag FF 3700) from the Las Piedras Basin was deposited in the collection of the Centro de Ornitología y Biodiversidad, Lima, Peru (CORBIDI).

Age classification, sex determination, and data analyses. To estimate the age class of *P. pipa* individuals we measured them using snout–vent length (SVL) (Duellman, 2005). Although precise age estimation is not possible for *P. pipa*, broad age-class assignment (juvenile vs. adult) is well supported by published size ranges (Rabb and Rabb, 1963; Duellman, 2005). We used SVL to help identify unique individuals, but here we refer to captures, not individuals, and do not assume individuality. Determining the sex of captured individuals was challenging due to the low degree of sexual dimorphism in *P. pipa* (Alves-Pinto et al., 2014). However, gravid females could be identified due to the characteristic honeycomb-like depressions or pockets in the dorsal skin where eggs are embedded during the breeding cycle (Rabb and Snedigar, 1960; Rabb and Rabb, 1960, 1963). To determine whether capture probabilities deviated from a random distribution, we applied a binomial test (Wagner-Menghin, 2014) incorporating the exclusive probabilities of dichotomous data derived from captures in buckets.

Results

Over 67 trap-nights, the Suriname and Skyfall traps captured a total of 18 *P. pipa* across 16 different nights, including four consecutive nights in late April 2013. Captured individuals ranged in SVL from 5.5–15.0 cm (mean = 11.0 cm, SD = 3.2 cm). We captured six *P. pipa* in the Suriname Trap, three of which were moving away from the lake, while none were captured on the upland side (Fig. 1B). In contrast, we captured 12 *P. pipa* in the Skyfall Trap, which operated for a longer duration. Most were found in Buckets 2 and 4, which were positioned to sample upland habitats, while none were caught in the buckets facing the lake (Fig. 1C). Additionally, four individuals were captured in Bucket 6, which was closer (~50 m) to flooded regions north of the lake, making it unclear whether these frogs were still moving inland or using nearby aquatic habitats. Notably, no *P. pipa* were captured in the opposing buckets in either trap. Assuming two unidirectional movements, a binomial test indicates a low probability ($p = 0.015$) that these results occurred by chance. The Skyfall Trap was associated with a significant effect ($p = 0.019$), while no significant effect was detected for the Suriname Trap ($p = 0.109$; Table 1). The normal distribution of snout-to-vent length (SVL) values in the Skyfall Trap ($n = 12$, Shapiro-Wilk $W = 0.936$, $p = 0.453$) suggests that the trap randomly captured individuals across different size classes, including both juveniles and adults.

No neonate *P. pipa* (SVL ≤ 4 cm) were captured during opportunistic searches or pitfall trapping, but two individuals were definitively identified as females, distinguished by the presence of large pores on the dorsal skin. One of these females was gravid, as confirmed when froglets spontaneously emerged upon her release into water (Fig. 2).

Although we had 18 total captures, it is possible that a single individual was captured twice based on having the exact same SVL. The overall lack of repeating SVL measurements, when paired with our protocol of release into the lake, suggests a low recapture rate. Our initial captures in the Suriname Trap occurred between major rain surges during the 2012 wet season (Fig. 3) and were evenly distributed throughout the short sampling period. By contrast, during the second sampling period

Table 1. Summary of *P. pipa* captures recorded at Suriname and Skyfall pitfall traps, showing capture date, snout-to-vent length (SVL, in cm), bucket placement (BP), habitat sampled (HS), and total captures (TC). Non-exclusive capture probability (NEP) refers to cases where the bucket position allowed potential captures from multiple habitat directions (e.g., lake or upland). Sum of non-exclusive captures (SNEC) represents the total probability-adjusted captures for each trap. Missing data (i.e., those that could not be collected) are indicated by a missing symbol (⃠), en-dashes (–) identify non-applicable entries.

Trap	Date	SVL	BP	HS	NEP	SNEC	TC
Suriname	05/11/12	⃠	2	Lake	–	–	–
	07/11/12	⃠	1	Lake/Upland	0.5	–	–
	12/11/12	⃠	4	Lake/Upland	0.5	–	–
	14/11/12	⃠	2	Lake	–	–	–
	17/11/12	⃠	1	Lake/Upland	0.5	–	–
	01/12/12	⃠	2	Lake	–	1.5	6
Skyfall	24/04/13	12.0	4	Upland	–	–	–
	26/04/13	14.5	6	Lake/Upland	0.5	–	–
	27/04/13	9.5	1	Lake/Upland	0.5	–	–
	27/04/13	6.2	4	Upland	–	–	–
	28/04/13	5.3	6	Lake/Upland	0.5	–	–
	05/05/13	12.2	2	Upland	–	–	–
	11/05/13	10.5	2	Upland	–	–	–
	12/05/13	15.0	2	Upland	–	–	–
	14/05/13	9.5	2	Upland	–	–	–
	14/05/13	9.0	4	Upland	–	–	–
	17/05/13	13.7	6	Lake/Upland	0.5	–	–
	31/05/13	14.0	6	Lake/Upland	0.5	2.5	12
Both	–	–	–	–	–	4.0	18

Figure 2. Gravid female *Pipa pipa* captured in the Suriname Trap at Las Piedras, Peru, on 14 November 2012. Photo by Harry F. Williams.

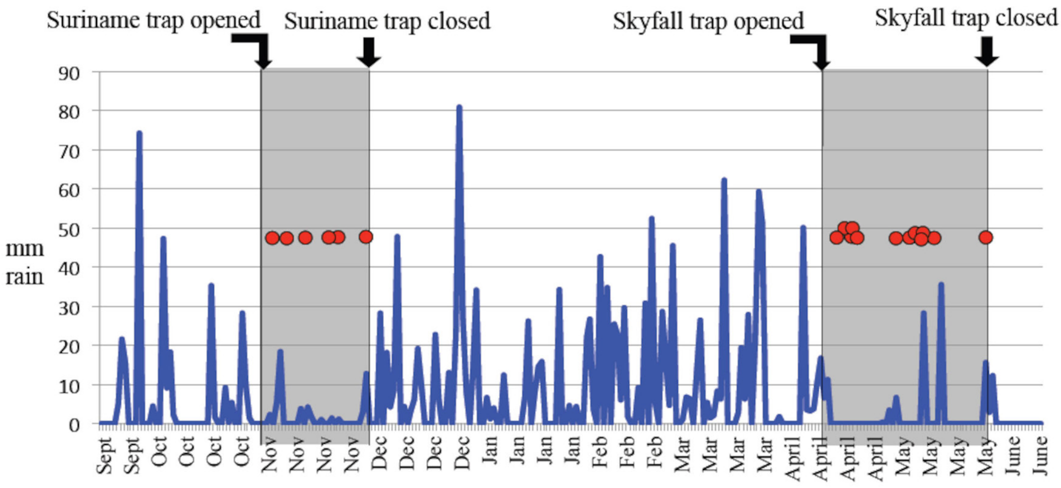

Figure 3. Daily rainfall (mm) and *Pipa pipa* captures recorded at Las Piedras, Peru, from September 2012–June 2013. The blue line represents daily precipitation, while red circles indicate *P. pipa* captures across 67 trap-nights, spanning 16 capture nights. The grey-shaded regions mark the operational periods of the two pitfall traps: Suriname Trap (November–December 2012, wet season) and Skyfall Trap (April–May 2013, late wet to early dry season). Captures at the Suriname Trap occurred between major rain surges, whereas Skyfall Trap captures were concentrated after peak rainfall, coinciding with the drying of upland swamps.

(Skyfall Trap), the majority of late-wet season rainfall had already occurred prior to trapping (Fig. 3). Despite this, we observed two distinct peaks in *P. pipa* captures, both of which coincided with the drying of upland swamps, suggesting a possible link between receding water levels and movement patterns.

Discussion

Our study provides direct evidence that *P. pipa* undergoes seasonal overland movements between intermittent wetlands and permanent waterbodies. During the dry season, individuals appear to be forced to migrate from drying wetlands to more stable aquatic habitats, such as lakes. This movement is reversed in the wet season, as flooded wetlands become available again. While opportunistic encounters have previously suggested occasional terrestrial activity (e.g., Duellman, 2005), our findings provide direct proof that this behaviour is not merely occasional but likely patterned after the availability of suitable, inundated habitat, with a total of 18 captures following this pattern. To our knowledge, this represents the largest number of *P. pipa* individuals recorded at a single site, regardless of previous research efforts (Buchacher, 1993; Rodriguez and Duellman, 1994; Parmelee, 1999; Duellman, 2005; Catenazzi et al., 2013; Upton et al., 2014; Silva et al., 2020).

Previous authors have suggested that *P. pipa* lacks coordination and effective locomotion on land, leading to the assumption that it rarely, if ever, leaves the water (Buchacher, 1993). However, our findings challenge this notion by showing that *P. pipa* engages in predictable, seasonal movement, likely driven by hydrological cycles rather than random dispersal. The presence of *P. pipa* in small, isolated waterbodies, located hundreds of meters from larger lakes or rivers, necessitates at least some degree of terrestrial dispersal. In this study, we provide direct evidence of overland movement, with individuals traveling at least 100 m, and potentially up to 300 m, across dry land.

It is also noteworthy that despite the existing documentation that *P. arrabali* colonises distant waterbodies (Gascon, 1992; Buchacher, 1993), neither these studies nor ours recorded direct observations of *Pipa* species moving on land. The absence of *P. pipa* captures in six of the trap arrays suggests that no terrestrial dispersal occurred between the two major waterbodies (river and lake). If frogs were moving to or from the lakeshore in that region, we would have expected to detect them in these traps. Based on this, we estimate the total usable lakeshore at Lago Soledad for *P. pipa* at approximately 2800 m. Our traps sampled only ~3% of this available habitat, covering just 80 m of drift line. The surveyed lakeshore includes associated upland floodplain forests, as well as permanent lakes and ponds that *P. pipa* may use when water levels permit. Additionally, our brief opportunistic observations of *P. pipa* at a second oxbow lake and a nearby swamp further support the presence of the species in multiple aquatic environments. The absence of direct sightings highlights a gap in our understanding of *P. pipa* terrestrial locomotion strategy. While its locomotor ability remains debated, our results indicate that overland movement is a regular part of its natural history, suggesting there is a mechanism or behavioural strategy that minimizes the cost of terrestrial dispersal.

Our rainfall data did not reveal a direct hydrological trigger for *P. pipa* movements. During the Skyfall Trap sampling period, no rain events were significant enough to raise water levels in inland swamps. This was not only due to low daily precipitation (≤ 50 mm per day) but also aligns with the typical seasonal flooding pattern in southeastern Peru during April–May (Goulding et al., 2003; Melack and Hess, 2010; Junk et al., 2011).

Because aestivation is unknown in *P. pipa*, we assume that annual drying of floodplain habitats would be fatal to individuals unable to reach permanent water. However, the motivation for movements out of the lake remains unclear. Despite this uncertainty, our results suggest that overland movement is a normal aspect of *P. pipa* ecology in Lago Soledad and other habitats with similar hydrological cycles. The two unidirectional movement patterns observed in this study indicate a migratory response to seasonal habitat constraints, rather than random dispersal (Bailey et al., 2004; Gamble et al., 2007). Notably, this migration does not appear to be age-specific, as individuals of varying sizes were recorded. We acknowledge that differentiating individuals based on SVL is imperfect, particularly when measurements are taken from live animals, as movement, posture variation, and handling constraints can introduce notable errors (Fitch, 1987; Qualls and Shine, 1998). Thus, some uncertainty remains regarding whether all captures represented unique frogs. Hypothetical recaptures would uphold a relevant spatial scale of hundreds of meters overland dispersal.

The gravid female *P. pipa* captured in the Suriname Trap (Fig. 2) represents a notable and unique observation for this study. This female was captured in the first bucket during the period of dispersal away from the lake, suggesting that at least some females undertake overland movement prior to the emergence of their offspring, despite the potential risks. While this behaviour could be interpreted as random dispersal (Semlitsch, 2008), it raises important questions about the reproductive ecology of *P. pipa* and the factors driving female movement. Further study is needed to better understand these movements and their implications for the natural history of the species.

The lakeshore habitat at Lago Soledad supports a diverse array of aquatic environments, yet only ~3% of its total shoreline length was covered by drift lines.

In the "superpopulation" model of Kinkead and Otis (2007), drift line length correlates with wetland shoreline measurements, providing a potential framework for estimating *P. pipa* habitat use. Additionally, the observed overland movements could indicate population viability, as movement between different wetlands may help sustain metapopulations (Semlitsch, 2008).

Based on our findings, we propose modifications to pitfall trapping methodology for future studies on *P. pipa* as follows: (1) Shallower traps (20–30 cm depth) can be used since a depth > 40 cm is unnecessary. (2) Fence height can be reduced to 30 cm because *P. pipa* is unlikely to require tall barriers to impede its terrestrial movements. (3) Escape structures, such as latticing with sticks or floating platforms, should be installed to prevent the entrapment of species capable of climbing. (4) There can be less emphasis on drainage efficiency when selecting and constructing sites, as high-water periods coincide with *P. pipa* movement. These design adjustments could facilitate mark-recapture studies and enable more robust population assessments of *P. pipa*, a species that is poorly studied yet likely very common.

Our study indicates a well-developed and potentially expanding local population of *P. pipa*. We therefore agree with considering *P. pipa* as a species of Least Concern according to IUCN Red List criteria. Moreover, our study highlights how similar trapping methodologies could be applied to rarer, highly cryptozoic species lacking a defined conservation status. By using these approaches, researchers can improve population assessments and conservation strategies for species that are otherwise difficult to study.

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