



# Habitat use of the micro-endemic day gecko *Phelsuma antanosy* in Sainte Luce, Madagascar, and the case for translocation

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**ABSTRACT:** The Critically Endangered day gecko *Phelsuma antanosy* is micro-endemic to 2 humid forest sites in southeastern Madagascar. At one of these, Sainte Luce, it inhabits 4 forest fragments, 2 of which are set to be cleared for mining. Translocation of individuals from within the mining path to protected forest fragments has been proposed to mitigate the impact of habitat loss and the resulting reduction in population size. However, lack of knowledge of its habitat requirements and population structure inhibits efforts to evaluate the likely ecological consequences of translocation. We sampled 92 *P. antanosy* individuals across each of the known subpopulations in Sainte Luce and assessed the habitat conditions in which they occur, alongside levels of morphological variation. Using 5 morphological trait measures, we found no evidence of subpopulation differentiation. Almost all (>87%) *P. antanosy* individuals were found on *Pandanus longistylus* plants and occupancy levels were higher in areas with moderate (30–60%) canopy cover and no other *Phelsuma* spp. present, suggesting that translocated individuals should be located into these conditions and within a short (<5 m) distance of *P. longistylus* plants. We propose that siting individuals in patches meeting these criteria may help to maximise translocation efficacy. We discuss our results in the context of the lack of ecological and genetic information on this species, the general need for long-term monitoring of threatened species and the utility of translocation projects to inform and benefit conservation science.

**KEY WORDS:** Conservation · Endangered species · Population genetics · Reptiles · Translocation

## 1. INTRODUCTION

Rapid, large-scale land-use and climate change in the Anthropocene have precipitated an extinction crisis, which threatens to become the Earth's 6th mass extinction event (Thomas et al. 2004, Barnosky et al. 2011, Ceballos et al. 2017, Otto 2018). Accelerating global declines in wildlife are being driven primarily by habitat destruction and fragmentation (Fahrig 2003, Newbold et al. 2016, IPBES 2019), though vul-

nerability to these processes varies widely among taxonomic groups (Purvis et al. 2000). Within this broad pattern of biodiversity loss, reptiles are among the worst affected taxa (Gibbons et al. 2000, Saha et al. 2018), with roughly 20% of species now threatened with extinction, and 5% of those considered Critically Endangered (Jenkins et al. 2011). As in other taxa, research on reptiles has shown that extinction risk, in response to fragmentation, is increased when dispersal is constrained (Sarre et al. 1995, Driscoll 2004) and

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Fig. 1. *Phelsuma antanosy* female (top) and male (bottom). The species is microendemic to littoral forest in southeastern Madagascar (Fig. 2). The sexes have similar markings, but females generally display less vivid colouration. Photo credits: Sam Hyde Roberts (top), Alex Tomb (bottom)

habitat requirements are more specific (Foufopoulos & Ives 1999, Lehtinen & Ramanamanjato 2006). As more species of reptiles are exposed to the threats of habitat loss and fragmentation, conservation actions that mitigate their effects become increasingly necessary.

Reptiles are generally understudied, particularly in the tropics, where their diversity is highest (Gardner et al. 2007). It is also here that patterns of land use are changing most rapidly (Winkler et al. 2021), with profound implications for wildlife communities. This is exemplified in Madagascar, a globally renowned biodiversity hotspot, celebrated for its high levels of endemism (Antonelli et al. 2022). Yet Madagascar is experiencing severe environmental change and associated biodiversity impacts, including among reptiles (Rakotomanana et al. 2013, Jones et al. 2019). The day gecko genus *Phelsuma* contains 43 species native to the islands of the Western Indian Ocean, with 29 being endemic to Madagascar (Rocha et al. 2009). One of these, *P. antanosy* (Fig. 1), is found only in the

forests surrounding the city of Tolagnaro. Very little is known about the general ecology or reproductive biology of the species, but it exhibits many of the characteristics known to elevate extinction risk; having small population size and range, limited dispersal capability and high habitat specificity (Raxworthy & Nussbaum, 2000). Consequently, *P. antanosy* is one of 3 species in the genus listed as Critically Endangered by the IUCN, with habitat destruction and population fragmentation cited as the threatening processes (Jenkins et al. 2011).

Only 2 sites are reported still to support *P. antanosy* populations: the first is the Ambatotsirongorongo massif, comprising 2 disconnected montagne forest fragments, and Sainte Luce, where its distribution is limited to just 4 littoral forest fragments (sea level forest on sandy substrate close to the coast; S6–S9 in Fig. 2; Raxworthy & Nussbaum 2000, J. B. Ramanamanjato pers. comm.). A third population may exist in the rainforests of Tsitongambarika. Its remoteness

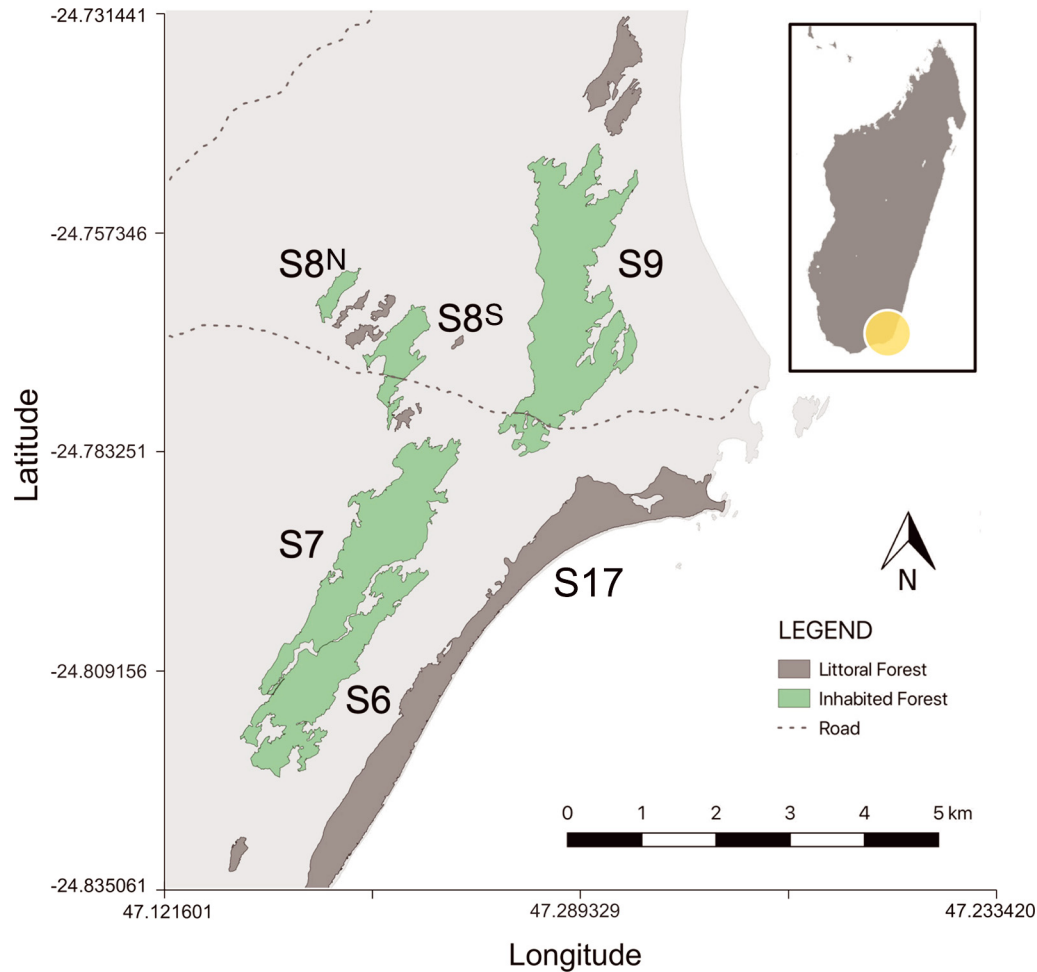


Fig. 2. Map of littoral forest fragments at Sainte Luce, Madagascar. The city of Tolagnaro (Fort Dauphin) lies ~30km to the southwest. Green fragments (S6, S7, S8north, S8south and S9) support populations of the Critically Endangered day gecko *Phelsuma antanosy*. Grey fragments are uninhabited, including the long coastal fragment S17, which does not support a population despite being apparently similar to inhabited fragments

makes this difficult to confirm; however there are no recorded sightings to date, and the site may be above the species' altitudinal limit (J. B. Ramanamanjato pers. comm.). Further population subdivision in Ambatotsirongorongo and Sainte Luce is thought likely due to fine-scale habitat fragmentation, especially in Sainte Luce, where forest fragments are separated by tracts of open savannah and cassava plantations, precluding dispersal. Of the 4 still inhabited fragments of Saint Luce (Fig. 2), two (S6 and S7) stand within the mining footprint of a large ilmenite mine operated by QIT Madagascar Minerals (QMM; Vincelette et al. 2007). Mining operations are set to begin in Sainte Luce before 2030 (P. Kluge pers. comm.). As a pre-condition to the mining project, managers are obliged to consider the impacts on wildlife, especially species considered to be of high conservation value. Given the recognition of *P. anta-*

*nosy* as an urgent candidate for conservation action (Raxworthy & Nussbaum 2000), an early '*Phelsuma antanosy* Action Plan' (Randrianantoandro et al. 2012) was drawn up by local stakeholders including QMM, and translocation was proposed as a plausible conservation strategy.

Translocation, or the intentional release of animals within their range in an attempt to augment a population, is increasingly being employed as a conservation tool in a variety of situations (Fischer & Lindenmayer 2000, Seddon 2010), with recent genomic evidence supporting its effectiveness (Capel et al. 2022). Yet, assessing the likely outcomes of translocation can be difficult (Weeks et al. 2011). It is widely recognised that knowledge of species' ecology, habitat requirements and genetic structure are key to implementing effective translocation and improving conservation outcomes more generally (Fischer &

Lindenmayer 2000, Agapow et al. 2004). Indeed, relocating individuals to unsuitable habitat has been identified as a reason for past failures in studies of translocation efficacy (Griffith et al. 1989).

Past rates of success in reptile translocations have been low relative to other taxa (Dodd & Seigel 1991), though this disparity may be narrowing (Fischer and Lindenmayer 2000). In addition, the purpose behind a translocation has a strong effect on its outcome, with those motivated by conservation far more likely to succeed than those undertaken to mitigate human–wildlife conflict (Germano & Bishop 2009).

The proposed mining operation in Sainte Luce was set to remove ~60% of the local forest, leaving ~626 ha intact (estimates are based on the best available information on mining extent [Vincelette et al. 2007, Temple et al. 2012] and our own GIS data on forest distribution). Although the *P. antanosy* subpopulations within this habitat (S6 and S7 in Fig. 2) would still be lost, importantly, a translocation could save its individuals. As well as the direct welfare benefit, translocating individuals to the remaining ~265 ha of suitable habitat (S8 and S9 in Fig. 2) would help to mitigate the negative impact to the species. This might be through bolstering the other subpopulations if they are below carrying capacity, or by expanding them in combination with habitat restoration to increase the carrying capacity. Although some small-scale and private translocations are thought to have already taken place, we have been unable to ascertain what was done, or whether any evaluation/monitoring occurred or is taking place. In view of the especially low success rate of such projects, and the generally recognised importance of ecological tailoring of translocation projects, effective action taken to translocate and conserve *P. antanosy* must be founded on knowledge of its fine-scale habitat use, population structure and demography, all of which are currently lacking.

Population structure is an important consideration when proposing conservation intervention. If populations are highly structured, subpopulations may be locally adapted and might benefit from being individually managed to maximise fitness and preserve maximum diversity (Conant 1988, Moritz, 1994, 1999, Storfer 1999). Phenotypic differentiation can be a key initial indicator of population structure, suggesting that sub-/populations are evolving independently. Therefore, we examined *P. antanosy* morphology to determine if there was any evidence of differentiation among the extant subpopulations. Morphological differences would suggest strong isolation and possible local adaptation that could be disrupted by admixture

between subpopulations, meaning that a translocation might have detrimental effects (Frankham et al. 2002).

In this study, we therefore investigate (1) the morphometric variation between the remaining independent subpopulations of *P. antanosy* in Sainte Luce and (2) the major ecological and habitat characteristics associated with *P. antanosy* presence, in order to identify key features of release sites and improve future translocation success. We combine discussion of our results with suggestions for a further research program that could benefit a translocation project and aid the conservation of this species.

## 2. MATERIALS AND METHODS

### 2.1. Surveys and sampling

Fieldwork was carried out within fragments of littoral forest located in Sainte Luce (Fig. 2), in the Anosy region of south-eastern Madagascar, between February and April 2018. Forest fragments (S6–S9 as designated by QMM [Vincelette et al. 2007]; Fig. 2) are separated by >1 km of unsuitable *Phelsuma antanosy* habitat, except for S6 and S7, which are separated only by a narrow swamp (<50 m). Due to the lack of any physical dispersal barrier between the latter 2 fragments, these are considered unlikely to house independent subpopulations. No morphometric samples were collected from S6, though it was included in habitat surveys. S8 is divided into S8north and S8south by a sand road, and of these, only S8north contains the species. As of 2023, S6 and S7 are due to be cleared by the mine, while S8 and S9 have protected status (Rarivoson 2007). Areas of S7 are being rapidly degraded by alteration to habitat associated with removal of timber for firewood and building materials, whereas S6 is relatively unexploited due to its inaccessibility. The term 'site' is used to refer to locations known to support *P. antanosy* (e.g. Sainte Luce), with 'fragment' used for areas of continuous forest within sites (e.g. S7). 'Population' is used to refer collectively to *P. antanosy* individuals inhabiting a site, and 'subpopulation' to individuals inhabiting a fragment.

*P. antanosy* uses the screwpine *Pandanus longistylus* for protection from predators and for foraging since invertebrates utilise its debris-filled leaf axils. A second *Pandanus* species, *P. dauphinensis*, is also facultatively used (not being essential to the species; Raxworthy & Nussbaum 1993), though details of this use remain unknown. *P. longistylus* plants are unevenly distributed within forest fragments at 2 spatial

scales, being totally absent from large areas and, in areas where they do occur, being clustered in small aggregations termed 'patches'. *Pandanus* spp. are predominantly gravity dispersed, hence each patch tends to comprise a large parent plant with its offspring, though larger patches may contain many generations and a mix of *P. longistylus* and *P. dauphinensis* individuals. These plants are so closely situated, and often overlapping, that we used patches rather than individual plants for assessing *P. antanosy* distribution. Pilot surveys suggested that individual plants constituting an obvious patch were commonly separated by <2 m. Therefore, where any *Pandanus* plant was separated from any other by <2 m, all those individuals were collectively defined as a single patch.

Surveying was carried out along transects between 8:00 and 15:00 h on dry days with minimal cloud cover (<20%). Elevation ranged between 2 and 4 m above sea level. Transects of between 150 and 500 m were carried out within each fragment to intersect areas where *Pandanus* plants occur. Only 1 transect was

carried out in S6, as this fragment had only a limited area containing *Pandanus*, while in S7–S9 there were 3, 4 and 3 transects, respectively. Where a *Pandanus* plant was located within 5 m of a transect, the extent of the patch was determined by locating all other *Pandanus* separated from it by <2 m, and from these by <2 m, until no further plants were within this range. Patches were thoroughly searched for *P. antanosy* and its presence or absence recorded. In occupied patches, habitat data were recorded (Table 1). GPS data were taken for all unoccupied patches surveyed and, when the total number of occupied patches sampled on the transect was known, habitat data were recorded from a random subset of the unoccupied patches, with sample size approximately equal to the sampled number of occupied patches on that same transect.

Habitat surveys on each (occupied or unoccupied) patch were as follows. First, the number of *P. longistylus* and *P. dauphinensis* plants in each of seven 0.5 m height categories was recorded. Due to the known importance of basking behaviour to small reptiles,

Table 1. Names, descriptions, units and relevant scales and analyses for all parameters recorded in 217 *Pandanus* spp. patches in forest fragments around Sainte Luce, Madagascar

Variable	Description	Unit	Level	Analysis
<i>Phelsuma antanosy</i> presence	Presence/absence of <i>P. antanosy</i> individuals	0/1	Patch	Habitat
<i>Pandanus</i> height	Mean of plant heights taken as the midpoint of their 0.5 m height category	m	Patch	Habitat
<i>Pandanus</i> structure	Coefficient of variation of <i>Pandanus</i> height	%	Patch	Habitat
Other <i>Phelsuma</i> spp.	Presence/absence of <i>P. lineata</i> or <i>P. parva</i> individuals within the patch	m <sup>2</sup>	Patch	Habitat
Canopy cover	Proportion ground area covered by vegetation at canopy height	%	Patch	Habitat
Distance to <i>P. longistylus</i>	Distance to the nearest <i>P. longistylus</i> from the patch centre (5 m categories)	m	Patch	Habitat
Plant species found on	Species of plant on which each <i>P. antanosy</i> individual was found		Individual	Habitat
Plant height	Height of the plant on which each <i>P. antanosy</i> individual was found	m	Individual	Habitat
Found height	Distance from the ground at which each <i>P. antanosy</i> individual was found	m	Individual	Habitat
Mass	Mass of each <i>P. antanosy</i> individual	g	Individual	Morphology
Vent-tail length	Distance from the vent to the tip of the tail of each <i>P. antanosy</i> individual	mm	Individual	Morphology
Snout-vent length	Distance from the vent to the tip of the snout of each <i>P. antanosy</i> individual	mm	Individual	Morphology
Head length	Distance from the tip of the snout to the rear of the parietal bone of each <i>P. antanosy</i> individual	mm	Individual	Morphology
Head width	Width of the head of each <i>P. antanosy</i> individual at the widest point	mm	Individual	Morphology
Sex	Sex of each <i>P. antanosy</i> individual, determined presence/absence of male-specific traits	male/female	Individual	Morphology

canopy cover was measured at 1 random point within the patch for every 10 m<sup>2</sup> of area it covered using a spherical densiometer. Distance to the nearest *P. longistylus* plant from the centre of the patch was recorded to the nearest 5 m, up to 30 m. We also noted the presence within patches of any of the 4 congeneric *Phelsuma* species: *P. lineata*, *P. parva*, and *P. modestus*.

When *P. antanosy* were observed, we recorded the plant species on which they were located. Age class (juvenile, sub-adult or adult) and sex were confirmed visually. Age was determined by a combination of colouration and sexual trait maturity characteristics (visibility of femoral pores), and sex by looking for male-specific traits (femoral pores anterior to the cloaca and brighter colouration). When possible, *P. antanosy* individuals were caught by hand and morphometric data collected (details in Table 1). Weight was estimated to the nearest 0.2 g by placing the individual in a plastic bag and using a Pesola scale. All length measurements were taken with electronic Vernier calipers to the nearest 0.01 mm. All measurements were made by the same researcher (M. D. Pointer), and each morphometric measurement was taken 5 times from the first 20 individuals caught to provide an estimate of repeatability. To enable future genetic investigations, tail tip tissue (~6 mm) was taken from 10 individuals per fragment (30 total) and stored in 90% ethanol at room temperature. Sterilising solution was applied to tails and sampled individuals were released at point of capture.

## 2.2. Statistical methods

All analyses were conducted in R v2021.09.1 (R Core Team 2013) unless otherwise specified.

In order to assess the repeatability of morphometric measurements, repeated measures of each morphometric trait for 20 adult individuals were entered in a general linear mixed model (LMM), with measurement value as the dependent variable and individual as a random factor, using the R package 'rptR' (Stoffel et al. 2017). Factor analysis was used to condense the measured morphometric variables into principal components (PCs). Morphological metrics from 60 individual geckos were tested for inter-fragment differences using a general linear model (LM) with the first principal component as the response variable and fragment ID as a predictor. Sex was also included to account for sexual dimorphism. S7 was selected as the fragment reference category as it is the source for proposed future translocations.

To assess the how patch-level habitat variables were related to *P. antanosy* patch occupancy across the 3 forest fragments, a generalised linear mixed model (GLMM), with a logit link function and binomial error term, was implemented using the R package 'lme4' (Bates et al. 2015), with *P. antanosy* presence/absence as the response variable, *Pandanus* height (mean of all height category midpoints per patch), *Pandanus* structure (coefficient of variation of height category midpoints), distance to the nearest *P. longistylus*, canopy cover (mean of all individual canopy cover measurements per patch) and presence of other *Phelsuma* species as fixed effects and fragment and transect as random effects (fragment was removed from the final model as it explained none of the variance in the response and prevented model convergence). Delta-adjusted marginal R<sup>2</sup> was calculated using the R package 'MuMIn v1.43.17' (Bartoń 2020) after the method of Nakagawa et al. (2017).

## 3. RESULTS

Surveyed patches numbered 217. In total, 121 *Phelsuma antanosy* were recorded in 112 unique occupied patches (14 in S6, 34 in S7, 37 in S8, 36 in S9). Of these, 92 were classified as adults (43 females and 49 males), 15 as sub-adults and 5 were juveniles. Morphometric data were collected from the 92 adults (30 in S7, 30 in S8, 32 in S9). No *P. antanosy* individuals were recorded in the remaining 105 randomly selected patches (these patches were across all fragments; 17 in S6, 21 in S7, 34 in S8, 33 in S9).

### 3.1. Morphological variation

All morphometric variables showed a high level of repeatability ( $R > 0.96$ ; Table A1 in the Appendix) except for upper hind limb length ( $R = 0.70$ ), which was therefore excluded from further analyses. Pearson correlations showed that all 5 remaining morphological variables (Fig. 3A–E) co-varied significantly ( $r = 0.56–0.79$ ). The Kaiser-Meyer-Olkin measure of sampling adequacy was 0.87, above the generally recommended 0.60 threshold, and the Bartlett's sphericity test result was significant ( $\chi^2(10) = 251.79$ ,  $p < 0.001$ ), making a good case for the use of factor analysis with these data.

Factor analysis of morphometric variables yielded a first principal component (PC1) with an associated eigenvalue of 3.54, explaining 70.84% of the total

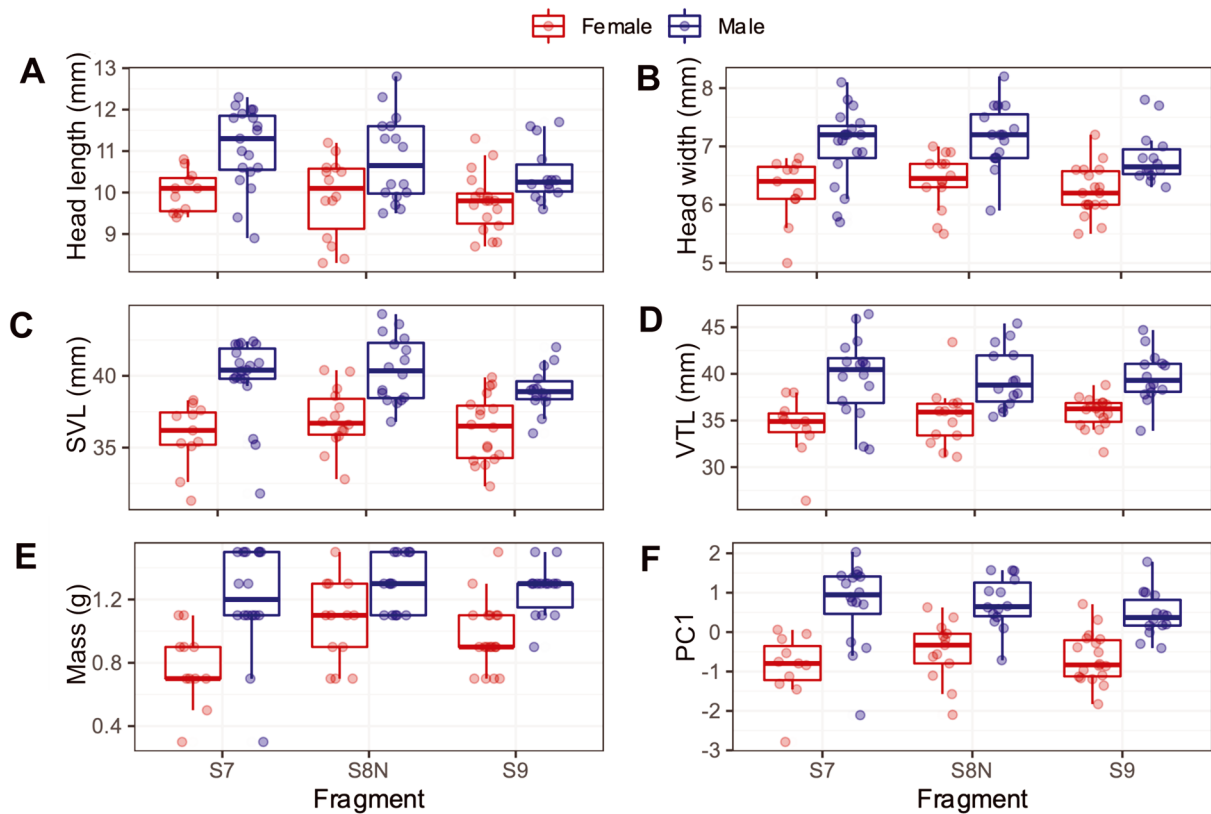


Fig. 3. Morphometric data of *Phelsuma antanosy* individuals in 3 forest fragments at Sainte Luce, Madagascar (S7:  $n = 30$ , S8north [S8N]:  $n = 30$ , S9:  $n = 32$ ). SVL: snout-vent length; VTL: vent tail length. (F): first principal component derived by factor analysis that captures 70.84% of variation across all measured morphological traits. Box height is interquartile range (IQR) of the data, whiskers show the range (excluding points  $>1.5 \times$  IQR outside the nearest quartile)

variance and strongly and positively associated with all 5 morphometric variables (Pearson correlation, all  $r \geq 0.75$ ). Subsequent PCs had eigenvalues of  $<0.6$  and each explained  $<12\%$  of the total variance. PC1 therefore represented a good estimate of overall body size for use in further morphometric analyses. We found no significant inter-fragment variation in PC1 (S7 vs. S8:  $\beta = 0.19$ , SE = 0.21,  $p = 0.35$ ; S7 vs. S9:  $\beta = -0.03$ , SE = 0.2,  $p = 0.88$ ), but a strong difference in PC1 between sexes ( $\beta = 1.29$ , SE = 0.17,  $p < 0.001$ ); with males larger than females (Fig. 3, F).

### 3.2. Habitat occupancy

In total, *P. antanosy* were found on 6 plant species and occupied 4 of those species in only a single fragment. Four of the 6 species were *Pandanus* spp., while the other 2 were bamby *Anthostema madagascariensis* and hazomainty *Diospyros* sp. Overall, 87.6% of individuals were found on *Pandanus* spp. (though this value was 94.6% in S8 and 100% in S9): 64.5% of all individuals were found on *P. longistylus* and 20.6% on

*P. dauphinensis*. Occupancy probability was also significantly greater in patches close to the nearest *P. longistylus* (80% of individuals found in patches with a *P. longistylus*  $< 5$  m from the patch centre), with intermediate canopy cover (93% of individuals found were in patches with 25–70% canopy cover) and with no other *Phelsuma* species present (Table 2; Fig. 4). All other *Phelsuma* species seen were *P. liniata* or *P. parva*.

Table 2. Generalised linear mixed model of patch occupancy by *Phelsuma antanosy* in relation to habitat characteristics of 217 *Pandanus* patches in forest fragments around Sainte Luce, Madagascar (model  $R^2 = 0.57$ )

Variable	$\beta$	SE	p
Intercept	4.54	1.03	$<0.001$
Canopy cover	-0.06	0.01	$<0.001$
Other <i>Phelsuma</i> presence	-1.21	0.41	$<0.003$
Distance to <i>P. longistylus</i>	-0.77	0.20	$<0.001$
<i>Pandanus</i> height	0.32	0.34	0.349
<i>Pandanus</i> structure	0.12	0.61	0.847

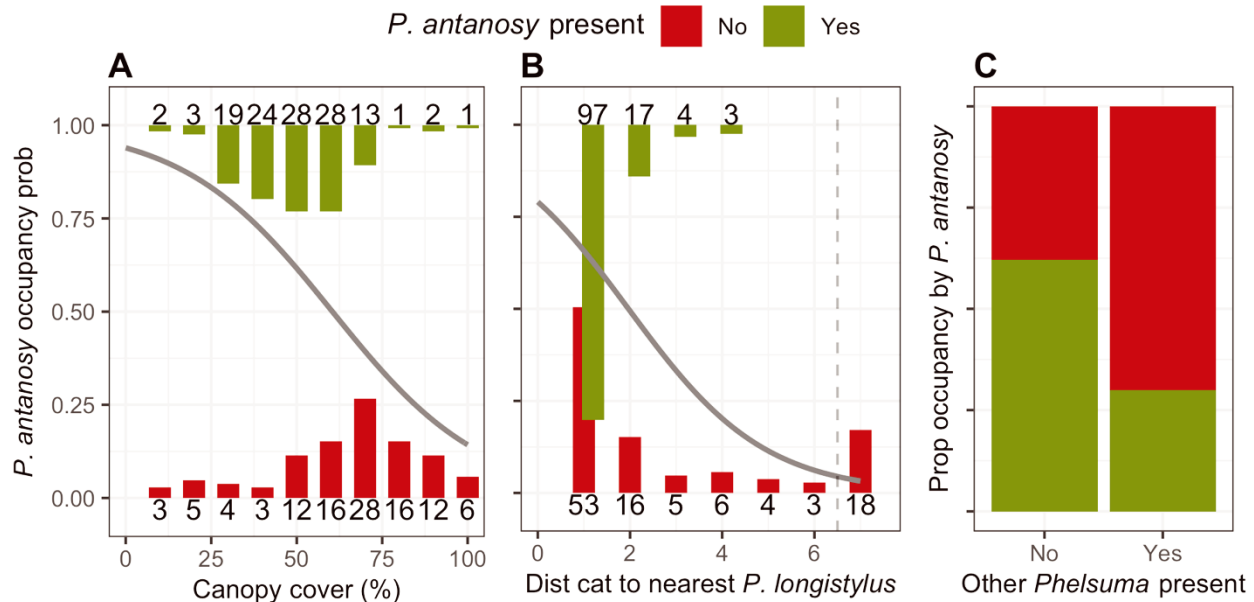


Fig. 4. Change in the probability (line) of *Pandanus* spp. patches being occupied by *Phelsuma antanosity* with varying levels of (A) canopy cover, (B) distance to the nearest *P. longistylus*. Coloured bars give the number of sampled patches that were occupied and unoccupied at each value of the x-axis. In (B) distances are categorised such that cat1 < 5; cat2 < 10; cat3 < 15; cat4 < 20; cat5 < 25; cat6 < 30; cat7  $\geq$  30 m). Panel (C) shows the proportion of occupied patches that did or did not have other *Phelsuma* species present

#### 4. DISCUSSION

*Phelsuma antanosity* is present in 4 littoral forest fragments in Sainte Luce, 2 of which (S6 and S7) are earmarked for clearance before 2030 as mining proceeds. Our results indicate no difference in morphometric character between the Sainte Luce subpopulations, and identify proximity to *Pandanus longistylus*, intermediate canopy cover and absence of other *Phelsuma* as important elements of microhabitat suitability.

The extent of suitable habitat for *P. antanosity* has been severely reduced at multiple scales. Forest continues to be lost across the region due to unsustainable human activity (Green & Sussman 1990; Vieilledent et al. 2018). On the Ambatosirongo massif, one forest fragment (Ambatosirongorongo), previously an important habitat for *P. antanosity*, has recently been completely cleared (S. Hyde Roberts pers. obs.), further reducing *P. antanosity* numbers and habitat. At a more local scale, it is not known when forest at Sainte Luce became fragmented, though evidence from fossil pollen in soil cores indicates that changing abiotic factors led to the current pattern of forest cover within the last 1000 yr (Virah-Sawmy et al. 2009). Regardless of timeframe, the forests of Sainte Luce are fragmented and continue to experience numerous threats, including

agricultural encroachment and resource extraction, and the forests are increasingly vulnerable to fire. Despite such fragmentation, we found no evidence for differences in morphological traits between individuals from different forest fragments. However, a consistent sexual size dimorphism was observed, a phenomenon which is only seen in a minority of gecko species and that appears to vary across the genus *Phelsuma* (Ikeuchi et al. 2005).

While we find no morphological evidence for population differentiation, other reptile species have shown genetic structure over similarly small scales (e.g. Dubey & Shine 2010, Buckland et al. 2014), and an appropriately robust population genetic investigation would strengthen the case for all Sainte Luce subpopulations constituting a single evolutionarily significant unit. Either single-nucleotide polymorphisms or microsatellite markers would help to determine the demographic and evolutionary forces at work in this population. However, a genome-wide approach would provide the best opportunity to identify functional variation and delineate units for conservation (Funk et al. 2012), and ideally would include individuals from all known populations in the range. In addition, genomic data would provide one means of obtaining population size estimates. Such demographic information could also be provided by a field study, improving the current understanding of



the size and density of subpopulations, as well as the species' conservation status.

In addition to information on population size and structure, ecological understanding is also important to translocation. Knowledge of habitat requirements aids the selection of suitable sites for translocation, in which environmental conditions are likely to facilitate subsequent survival and successful reproduction (Griffith et al. 1989). Past work on the efficacy of translocation projects has highlighted the role of release of translocated individuals into unsuitable habitat as a key cause of poor long-term outcomes (Griffith et al. 1989, Fischer & Lindenmayer 2000). Further, the quality of the release habitat for the species of concern is repeatedly shown to be the most important factor in reptile translocation success, yet conflict-mitigation translocations often suffer from poor habitat suitability of release sites (Dodd & Seigel 1991, Germano & Bishop 2009).

In order that a translocation of *P. antanosy* might avoid such pitfalls, and to improve the chances of success, we have identified microhabitat features that are particularly important for selected recipient sites. Locations containing *P. longistylus* plants, with moderate canopy cover and uninhabited by other *Phelsuma* species, are the microhabitats most commonly occupied in inhabited forest fragments. The importance of *Pandanus* spp. (especially *P. longistylus*) presence supports previous work on *P. antanosy*'s association with this species, which is considered critical for completion of its lifecycle (Raxworthy & Nussbaum 1993, Lehtinen 2002). Additionally, the necessity of a somewhat open canopy likely reflects the known importance of thermoregulatory behaviours in *Phelsuma* (e.g. Raxworthy 1988, Bungard et al. 2014).

These results are consistent with previous suggestions that *P. antanosy* is a habitat specialist species with narrow habitat requirements (Raxworthy & Nussbaum 2000). However, our findings also emphasise the potential importance of inter-specific competition in the species' ecology. Our morphological analysis showed sexual size dimorphism, which is often indicative of territorial behaviour (Ikeuchi et al. 2005) and *P. antanosy* was more likely to be found in the absence of congeneric individuals. Other species of this genus are known to be territorial (e.g. Wanger et al. 2009) and, even if *P. antanosy* is not itself territorial, given that it is the smallest of those present in the area, it may be more easily displaced from contested territories. Therefore, some component of *P. antanosy*'s association with *P. longistylus* may be due to competitive exclusion through interactions with congenics.

As previously mentioned, *P. antanosy* is little-studied and even relatively basic features of its ecology and reproductive biology are almost completely unknown. The competitive interactions discussed above are just one example of how further research could be of great benefit to a translocation program. Further understanding of both inter- and intra-specific competition, combined with data on current population densities and sex ratios, would inform optimal release densities. Quantifying current sex ratios would also aid understanding of the reproductive biology of *P. antanosy*, another area where little information is available at present. The timing and length of the breeding season, annual reproductive output and offspring survival rate would all provide valuable insight to assist proposed conservation actions. Together with adult survival rates, this information could be used to forecast how the population might grow following translocation, as a benchmark for monitoring activities. There is scope for such studies to be conducted observationally in natural populations at Sainte Luce, though for some traits it may be beneficial to bring some individuals into captivity or to maintain semi-wild populations in mesocosm cages encompassing natural habitat. The imminent nature of the threat to these forests means that the need for translocations is urgent, and while more time would bring additional data, this must be balanced against the need to act quickly. As such, the best course may be to combine a conservation intervention with work to quantify these key demographic and behavioural processes.

Releasing translocated individuals into recipient locations sharing the specific habitat characteristics that we have identified should hopefully enhance the survival probability and long-term success of any new subpopulation. Given the high habitat specificity of *P. antanosy*, and the great importance of habitat quality to translocation success (Griffith et al. 1989), areas receiving translocated individuals may also need to be managed to increase the amount of suitable habitat available. Future restoration initiatives should also consider translocating both *P. longistylus* and *P. antanosy* into new regions of the protected forest fragments S8 and S9 to increase the area of occupancy and improve the long-term survival prospects of both species. Additionally, the large fragment S17 (Fig. 2) could be investigated — it is not known why no *P. antanosy* subpopulation occurs there despite its being apparently similar to inhabited fragments. However, if the habitat is suitable, or could be made suitable through management, this would greatly expand the area of available habitat for translocation.

Another key component in enhancing the success of any translocation project is an ongoing monitoring regime that feeds back into management policies (Dodd & Seigel 1991). Too few conservation projects can maintain financial or political investment over a long enough period to provide sufficient monitoring. This can negatively impact both individual project outcomes and our wider understanding of which interventions do and do not work within the field of conservation science. *P. antanosy* has an opportunity to buck this trend. Within the Tolagnaro region, there are several stakeholders that are well situated to coordinate the management plan which must necessarily accompany any intervention as best practice. Further, as an attractive species that is widely recognised as one of the world's most endangered reptiles (Zoological Society of London 2024), and in a country that receives acclaim as a biodiversity hotspot, a successful conservation project has the potential to stimulate further biodiversity works and even shift perceptions; increasing pressure to prevent mining in environmentally sensitive areas.

In summary, we have shown that *P. antanosy* populations at Sainte Luce are morphologically undifferentiated, supporting the case for a conservation translocation for the avoidance of human–wildlife conflict. We also identify habitat characteristics associated with *P. antanosy* presence that may be used to identify suitable release sites. In addition, we have identified areas of further research, including population genomics as well as fundamental studies of ecology and life-history, that would maximise the success of a conservation intervention in this species.

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### Appendix

Table A1. Results from tests of repeatability of morphometric measurements of 60 *Phelsuma antanosy* individuals each measured 5 times

Variable	R (SE)	Lower CI	Upper CI	Median of CIs
Head width	0.95 (0.02)	0.86	0.97	0.92
Head length	0.96 (0.02)	0.91	0.98	0.95
Snout-vent length	0.97 (0.01)	0.94	0.99	0.97
Vent-tail length	0.98 (0.01)	0.96	0.99	0.98
Upper hind limb length	0.70 (0.09)	0.49	0.82	0.66
Weight	0.97 (0.01)	0.94	0.97	0.96

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