**Recent and rapid colonization of the Lesser Sundas Archipelago from adjacent Sundaland
by seven amphibian and reptile species**

SEAN B. REILLY^{1*}, ALEXANDER L. STUBBS¹, BENJAMIN R. KARIN¹, EVY ARIDA²,
DJOKO T. ISKANDAR³, JIMMY A. MCGUIRE¹

¹ Museum of Vertebrate Zoology and Department of Integrative Biology, University of
California, 3101 Valley Life Sciences Building, Berkeley, CA 94720-3160 USA

² Museum Zoologicum Bogoriense, Indonesian Institute of Sciences (LIPI), Jalan Raya Bogor-
Jakarta Km. 46, Cibinong 16911, Indonesia

³ School of Life Sciences and Technology, Institut Teknologi Bandung, Bandung 10, Jalan
Ganesa, Bandung, Java 40132, Indonesia

*corresponding author

Sean B. Reilly

Department of Ecology & Evolutionary Biology

University of California at Santa Cruz

130 McAllister Way, Santa Cruz, CA 95060

E-mail: sreilly@ucsc.edu

Abstract

The Lesser Sundas Archipelago is comprised of two parallel chains of islands that extend between the Asian continental shelf (Sundaland) and Australo-Papuan continental shelf (Sahul). These islands have served as stepping-stones for taxa dispersing between the Asian and Australo-Papuan biogeographic realms. While the oceanic barriers have prevented many species from colonizing the archipelago, a number of terrestrial vertebrate species have colonized the islands either by rafting/swimming or human introduction. Here we examine phylogeographic structure within the Lesser Sundas for three snake, two lizard, and two frog species that each have a Sunda Shelf origin. These species are suspected to have recently colonized the archipelago, though all have inhabited the Lesser Sundas for over 100 years. We sequenced mtDNA from 230 samples to test whether there is sufficiently deep genetic structure within any of these taxa to reject human-mediated introduction. Additionally, we tested for genetic signatures of population expansion consistent with recent introduction, and estimated the ages of Lesser Sundas clades, if any exist. Our results show little to no genetic structure between populations on different islands in five species, and moderate structure in two species. Nucleotide diversity is low for all species, and the ages of the most recent common ancestor for species with monophyletic Lesser Sundas lineages date to the Holocene or late Pleistocene. These results support the hypothesis that these species entered the archipelago relatively recently and either naturally colonized or were introduced by humans to most of the islands within the archipelago within a short time span.

1 | INTRODUCTION

The oceanic islands of Wallacea are united by their historical isolation from the land masses of the Sunda Shelf to the west and the Sahul Shelf to the east and south (Figure 1). While oceanic islands tend to have lower biodiversity than adjacent continental regions, they also tend to have a higher proportion of endemic species in part because terrestrial fauna must cross oceanic barriers in order to colonize them making successful colonization rare and gene flow to and from the island low (Whittaker & Fernández-Palacios, 2007). Many other factors also influence the species diversity on oceanic islands such as their distance from continental sources, the presence or absence of intervening stepping-stone islands, island size, habitat heterogeneity, elevation, latitude, age, etc. (MacArthur & Wilson, 2001; Whittaker & Fernández-Palacios, 2007). However, since humans began maritime travel, the accumulation of species by human-mediated introduction has had an immense impact on the species diversity of islands worldwide (see Austin, 1999; Caphina *et al.*, 2015).

The Lesser Sundas Archipelago, comprising the southern portion of Wallacea, is composed of two parallel, linearly-arranged chains of oceanic islands, the oldest of which have been continuously emergent for 10-12 Ma (Hall, 2009). This long period of isolation provided ample time for natural colonization of the islands, as well as for *in situ* diversification, and the Lesser Sundas are consequently home to many endemic species (Orne *et al.*, 2005). Recent studies of Lesser Sundas amphibians and reptiles have shown that many of these endemics can be expected to exhibit deep inter- and intra-island divergences that reflect the complex tectonic history of the archipelago (Reilly, 2016; Reilly *et al.*, 2019). Although much of the diversity of the Lesser Sundas originated via natural processes, the archipelago has been inhabited by sea-faring humans for over 40,000 years, and these humans maintained a long tradition of pelagic fishing and trade between islands (O'Connor *et al.*, 2011). Indonesia is currently the fourth most populous country on earth and traveling and movement of goods between islands is still commonly undertaken by boat (Monk *et al.*, 1997). The long period of habitation by sea-faring humans has resulted in substantial human-mediated dispersal of plants and animals, including many reptile and amphibian species, throughout the archipelago (Heinsohn, 2003; Reilly *et al.*, 2017).

Many species of reptiles and amphibians have become highly invasive due to human-mediated dispersal with major impacts on native fauna (Kraus, 2015). In the Lesser Sundas, this

phenomenon is easily observable by simply boarding one of the many ferries that traverse the archipelago, upon which multiple species of small geckos can be seen crawling on the walls of the ship. However, there are a number of other species of reptiles and amphibians in the Lesser Sundas with colonization histories that remain unclear. Here we examine seven species of reptiles and amphibians, each occurring on most of the major islands (Figure 2), that have either been shown to be recently introduced into other regions or are suspected of being moved between islands in the Lesser Sundas (Heinsohn, 2003). Nevertheless, these seven species have occupied islands within the archipelago for at least 100 years, indicating that they either arrived via human-mediated introduction before the early 1900's (see van Lidth de Jeude, 1895; Boulenger, 1897; Barbour, 1912; De Rooij, 1917a, 1917b; van Kampen, 1923; Mertens, 1930), or that they arrived via natural colonization.

Here we utilize mtDNA sequence data from 230 newly sequenced samples, along with existing data, to examine the phylogeographical structure in these seven species of reptiles and amphibians with the goal of determining if there is sufficiently deep genetic structure within the Lesser Sundas to reject the hypothesis that they were introduced by humans. We pursue this goal by estimating summary statistics useful for the detection of recent population expansions consistent with recent introductions, estimating the age of monophyletic Lesser Sundas lineages, and generating phylogenies that can shed light on the biogeographical history and any possible phylogeographic structure within the archipelago.

2 | MATERIALS & METHODS

2.1 | *Focal taxa*

Lycodon capucinus (Family: Colubridae). The common wolf snake has been shown to be invasive to many regions of Southeast Asia (Fritts, 1993; O'Shea *et al.*, 2018). Because sampling of this species within Indonesia is sparse, it remains unclear whether *L. capucinus* occurs naturally in the Lesser Sunda Islands.

Lycodon subcinctus (Family: Colubridae). The white-banded wolf snake also occurs throughout the Lesser Sundas and is similar in size and ecology to *L. capucinus*, suggesting it may have been transported between islands by human activity.

Trimeresurus insularis (Family: Viperidae). The venomous white-lipped island pitviper is widespread throughout the archipelago and exhibits regional color morphs that are consistent with long term isolation (see de Lang, 2011; personal observation). However, limited genetic analyses have found low divergence among island populations (How *et al.*, 1996; David *et al.*, 2003; Malhotra & Thorpe, 2004) suggesting the possibility of recent colonization or recent movement between islands.

Gekko gecko (Family: Gekkonidae). Tokay geckos occur throughout the Indo-Australian archipelago and a study based on limited sampling found minimal genetic divergence between Timor and multiple Sunda Shelf localities (Roesler *et al.*, 2011). This species is commonly found in human settlements and its prey, insects and smaller geckos, are abundant on boats travelling between islands.

Eutropis multifasciata (Family: Scincidae). Sun skinks were shown to be recently introduced to other regions of eastern Indonesia, and even to Australia and the USA (Ingram, 1987; Meshaka *et al.*, 2004; O'Shea *et al.*, 2018). A study based on allozyme data found limited divergence between islands within the Lesser Sundas suggesting that inter-island movement may be prevalent (Schmitt *et al.*, 2000). *Eutropis multifasciata* from the nearest Sunda Shelf island, Bali, was once considered a distinct subspecies (*E. m. balinensis*) from Lesser Sundas populations (*E. m. multifasciata*) based on scale morphology and coloration, though these subspecies have since been synonymized (Mertens, 1927, 1930; Auffenberg, 1980).

Polypedates leucomystax (Family: Rhacophoridae). The common tree frog has been shown to be introduced to various parts of Indonesia and the Philippines (Brown *et al.*, 2010). However, relatively high genetic diversity on neighboring Java combined with limited sampling from the Lesser Sundas has left their colonization history in the Lesser Sunda Islands an open question (Kuraishi *et al.*, 2013).

Kaloula baleata (Family: Microhylidae). The smooth-fingered narrow-mouthed frog is common throughout the Sunda Shelf and the Lesser Sundas. The close relative *K. pulchra* is suspected to

have been introduced to multiple islands in Wallacea including Flores, suggesting that *K. baleata* may also have been introduced via human activity (Whitten *et al.*, 1987; Heinsohn, 2003).

2.2 | Sampling

Herpetological surveys were conducted over the course of five expeditions between 2010-2014 on the islands of Bali, Nusa Penida, Lombok, Sumbawa, Flores, Lembata, Pantar, Alor, Wetar, Timor, Rote, Savu, and Sumba. Sampling information for each species can be found in Table 1 and a list of all newly sequenced samples and their localities can be found in Table S1. Voucher specimens and tissue samples are housed at either the UC Berkeley Museum of Vertebrate Zoology (MVZ) or the Museum Zoologicum Bogoriense (MZB) in Cibinong, Indonesia.

2.3 | Data collection

Genomic DNA was extracted from liver or tail tip tissues using the Qiagen DNeasy blood and tissue kit (Qiagen, Valencia, CA, USA). For *T. insularis*, two mitochondrial genes, *ND4* and *cytochrome b*, were PCR-amplified following standard procedures using the primers ND4 and LEU for the *ND4* gene (Arévalo *et al.* 1994), and the primers THRSN2 and H14910 for the cytochrome b (*cytb*) gene (Burbrink *et al.* 2000). The *cytb* gene was sequenced for both species of *Lycodon* using the primers THRSN2 and H14910. The *ND4* gene was sequenced for both *E. multifasciata* and *G. gecko* using the primers ND4 and LEU. The *I6S* gene was sequenced for *P. leucomystax* and *K. baleata* using the primers 16sc-L and 16sd-H (Evans *et al.*, 2003). PCR reactions were carried out using standard Sanger sequencing methods, and ethanol precipitation. DNA sequence visualization was performed on an ABI 3730 automated sequencer (Applied Biosystems, Foster City, CA, USA). Forward and reverse sequence reads were combined in GENEIOUS V11.1.5 (<https://www.geneious.com>). For each species, relevant DNA sequence data (i.e., for samples from the Lesser Sundas or other Sunda Shelf localities) were downloaded from GenBank. Sequence alignments were generated using MUSCLE (Edgar, 2004) with manual corrections where necessary.

2.4 | Data analysis

The software JMODELTEST 2 (Darriba *et al.*, 2012) was used to infer the appropriate models of sequence evolution for phylogenetic analyses. Maximum Likelihood phylogenetic analysis was carried out using the program RAXML v8 (Stamatakis, 2014) with node support assessed with 1,000 nonparametric bootstrap replicates. For monophyletic Lesser Sundas clades with phylogenetic structure, the timing of entry into the archipelago was roughly estimated using the software BEAST v2.4.8 (Bouckaert *et al.*, 2014) with a strict molecular clock applied and a rule of thumb 2% divergence/million years sequence evolution rate-calibration. For BEAST analyses, a data matrix composed of one sequence per unique haplotype was subjected to two separate runs of 10 million generations or more (in order to ensure parameter ESS values were >200). To obtain divergence estimates, the results of each pair of analyses were combined after discarding 10% of the samples as burn-in.

Summary statistics including number of haplotypes, parsimony informative sites, haplotype diversity, nucleotide divergence, Tajima's *D* (Tajima, 1989), and Fu's *F_s* were calculated with the software DNASP v5 (Librado & Rozas, 2009). Tajima's *D* (when significantly negative) and Fu's *F_s* statistics can detect a rapid population expansion after a genetic bottleneck. All sequences are deposited in GenBank (accession numbers available upon acceptance).

3 | RESULTS

3.1 | Genetic structure

Kaloula baleata exhibits substantial genetic structure (Fig. 3a). Samples from Timor are nested within samples from Java and Bali. This "Java/Bali/Timor" clade is sister to a Lesser Sundas clade containing samples from Sumbawa, Sumba, and Flores. The haplotype of the Bali sample is identical to that of two samples from Timor. Frogs from Sumbawa form a monophyletic assemblage with high support (bootstrap=94).

Within *P. leucomystax*, the Lesser Sundas samples are most closely related to samples from Java, Bali, and Nusa Penida (Fig. 3b). A single common haplotype is shared across every island sampled within the Lesser Sundas as well as Java and Bali.

Within *E. multifasciata*, our single sample from Timor is sister to a Bali clade, though still highly divergent. This Bali/Timor clade is sister to all remaining samples forming a well-

supported Lesser Sundas clade (bootstrap proportion=100) (Fig. 3c). These two haplotype groups are differentiated by ~4% sequence divergence at the *ND4* gene. Within the Lesser Sundas, lizards from Wetar and Pantar each form monophyletic groups, though only supported by one informative mutation for each clade. A single common haplotype is found on Lombok, Sumbawa, Flores, and Alor.

Samples of *G. gecko* from the Lesser Sundas are found in three separate clades each comprised of a collection of samples representing multiple overlapping localities. For example, samples from Sumbawa are present in each of the three clades. One of the two samples from China is nested in amongst the three Lesser Sundas clades and a second sample from China is sister to all other samples (Fig. 3d). The only monophyletic island is Bali, united by a single shared mutation. One common haplotype is found on Nusa Penida, Sumbawa, Sumba, Sabu, and Timor, while a second common haplotype is found on Sumbawa, Flores, Pantar, Alor, Wetar, Timor, and Rote.

Lycodon capucinus samples from the Lesser Sundas contain a total of three haplotypes distinguished by two parsimony informative substitutions. The most common haplotype was found in samples from Malaysia, Sumbawa, Flores, Pantar, Alor, Wetar, Timor, Rote, Sabu, and Christmas Island (Fig. 3e). A second haplotype occurs on Christmas Island and Flores, and a third haplotype occurs on Bali and Sumbawa.

Within *L. subcinctus*, a total of two haplotypes were recovered from the eight newly sequenced samples with only one singleton mutation found in a Flores sample (Fig. 3g). The common haplotype was found in snakes from Lombok, Sumbawa, Flores, Lembata, and Pantar. The Lesser Sundas samples form a strongly supported clade relative to samples from Malaysia, Thailand, and the Philippines, but we lack samples from adjacent Java or Bali.

A total of 11 haplotypes were recovered from the 57 *T. insularis* samples with only three parsimony informative sites present. The most common haplotype, belonging to 40/57 Lesser Sunda samples, is found on every island except Lombok. Lombok is the only monophyletic island population and is differentiated by a single unique mutation (Fig. 3f). A *T. insularis* sample from eastern Java is sister to all Lesser Sundas samples. *Trimeresurus fasciatus* from Tanahjampea Island (123 km north of Flores) was found to be the sister taxon of *T. insularis*.

3.2 | Summary statistics

Within the Lesser Sundas samples, genetic variability ranged from a low of one variable site and no parsimony informative sites (*L. subcinctus*) to a high of 54 variable sites with 10 parsimony informative sites (*E. multifasciata* “Lesser Sundas” clade + Timor sample) (Table 1). However, when *E. multifasciata* samples from the Lesser Sundas without Timor are considered there are only 23 variable sites, eight of which are parsimony informative. Haplotype diversity within Lesser Sundas samples ranged from 0.10 (*P. leucomystax*) to 0.91 (*E. multifasciata* “Lesser Sundas” clade) (Table 2). Nucleotide diversities within Lesser Sundas samples were all low and ranged from a low of 0.0002 (*P. leucomystax* and *L. subcinctus*) to a high of 0.0044 (*G. gecko*) (Table 2). Tajima’s D statistics calculated from Lesser Sundas samples were negative for all species, ranging from -0.58 (*K. baleata*) to -2.20 (statistically significant value for *E. multifasciata* “Lesser Sundas” clade). Fu’s *F_s* statistics were negative for all Lesser Sundas samples, ranging from -0.18 (*L. subcinctus*) to -16.52 (*E. multifasciata* “Lesser Sundas” clade), while the clades of *E. multifasciata* and *K. baleata* containing samples from Timor and Bali had positive values (2.55 and 1.02, respectively).

3.3 | Ages of Lesser Sundas clades

The ages of the most recent common ancestors (MRCA) of each Lesser Sundas clade fell within the late Pleistocene (even considering 95% confidence intervals) with a range of 80,000-490,000 years (Figure 3). For the frogs, MRCA age was estimated for the Lesser Sundas clade (not including Timor) of *K. baleata* (0.49 Ma; 95% CI 0.31-0.69 Ma), and no estimate is given for *P. leucomystax* due to the nested Sundaland samples from Java, Bali, and Nusa Penida. Among lizard species, MRCA ages were estimated for the Lesser Sundas lineage (not including Timor) of *E. multifasciata* (0.42 Ma; 95% CI 0.26-0.60 Ma), and for two lineages of *G. gecko* that contain mostly Lesser Sundas samples: 1) a lineage containing samples from Sumbawa, Flores, Sumba, Sabu, Timor, and Nusa Penida (0.16 Ma; 95% CI 0.06-0.27 Ma), and 2) a lineage containing samples from Sumbawa, Flores, Pantar, Alor, Wetar, Timor, Rote, and Bali (0.17 Ma; 95% CI 0.07-0.27 Ma). Within snakes, MRCA ages were estimated for Lesser Sundas lineages of *L. subcinctus* (0.08 Ma; 95% CI 0.003-0.18 Ma) and *T. insularis* (0.19 Ma; 95% CI 0.11-0.30 Ma), and no estimate is given for *L. capucinus* because no monophyletic Lesser Sunda lineage exists.

4 | DISCUSSION

4.1| *General patterns*

The mitochondrial markers we have screened are well-suited for rejecting human-mediated introductions since deep genetic structure would indicate that their occurrence in the region predated the arrival of humans. However, lack of structure does not necessarily mean that these species did not arrive via natural dispersal. We set out to determine if there was sufficiently deep genetic structure within these taxa to reject the hypothesis that the Lesser Sundas populations are the result of human introductions. However, one potential complication is that independent introductions from structured populations outside of the Lesser Sundas could be misinterpreted as structure within the Lesser Sundas. Adding to this challenge is the possibility that some taxa may be composed of both native and non-native populations.

If any of these species had been long-established in the Lesser Sundas, we would expect each island population, or at least sets of islands, to have unique mutations resulting in phylogeographic structure. The results of our mitochondrial phylogenetic estimates and summary statistics have shown that each of the seven focal species have little to moderate genetic differentiation and little to no phylogeographic structure across the oceanic islands of the Lesser Sundas. This pattern could be created by different scenarios, four of which are considered here: 1) natural introduction with prolific recent natural dispersals between islands, 2) natural introduction with human-mediated dispersal between islands, 3) a single human mediated introduction and human-mediated dispersal between islands, or 4) multiple human-mediated introductions and human-mediated dispersal between islands.

While our MRCA ages are only rough estimates, they do suggest that some species may have occurred within the Lesser Sundas on the order of hundreds of thousands of years, and the negative Tajima's D values estimated for Lesser Sundas samples within each species are consistent with recent population expansions. Given that each of these species is known to have occurred throughout the majority of their currently known Lesser Sundas range for over 100 years, any human mediated introductions into the archipelago or specific islands would have occurred before the 20th century (Table S2). While a primary goal of this study was to search for evidence of a natural invasion for these taxa, we can reject human-mediated introduction to the archipelago for only *K. baleata*, *E. multifasciata*, and *T. insularis*. Even for these taxa, the

general absence of phylogeographic structure within the Lesser Sundas indicates that we cannot reject recent human-mediated inter-island dispersal.

4.2 | *Candidates for natural introduction with possible human-mediated dispersal*

The white-lipped island pitviper has very low genetic diversity with a common haplotype found on every island except Lombok. However, *T. insularis* does contain some phylogeographical structure with Lombok island samples forming a monophyletic group. Although the topology of our tree places samples from Wetar plus Pantar as basal within the Lesser Sundas, support for this branching pattern is very weak and it is more appropriate to interpret the tree as a large polytomy or star phylogeny. *Trimeresurus insularis* diverged from its sister species *T. fasciatus*, which is found on Tanahjampea Island to the North of Flores, approximately 2.4 Ma. It is unclear if the ancestor of these two species dispersed from Tanahjampea to the Lesser Sundas, or from the Lesser Sundas to Tanahjampea, but the prevailing north-to-south oceanic currents in the Flores Sea suggest that a dispersal from Tanahjampea to the Lesser Sundas is more likely (Gordon, 2005). If this is the case, then East Java may have been colonized by *T. insularis* from the Lesser Sundas. While it appears that this species has naturally occurred in the archipelago for some time, we note that both the high densities of *T. insularis* and the movement of large quantities of agricultural goods by boat could potentially transport these pitvipers between islands.

Both *Kaloula baleata* and *Eutropis multifasciata* have moderate phylogeographic structure and genetic diversity within the Lesser Sundas suggesting that they have inhabited the archipelago for at least thousands of years. Interestingly, for both species, our data indicate that samples from Timor are more closely related to samples from Bali (and Java in the case of *Kaloula*) than to samples representing the remainder of the Lesser Sundas. An important difference between these species, however, is that the *K. baleata* sample from Bali had an identical haplotype to some Timor samples, whereas the *E. multifasciata* sample from Timor is clearly divergent and quite genetically distinct from samples from Bali. This suggests that *K. baleata* likely arrived on Timor via human-mediated introduction from Bali, whereas *E. multifasciata* on Timor may very well represent a separate natural introduction from Bali or elsewhere. Regarding the non-Timor populations of *Kaloula* in the Lesser Sundas, our limited

data set exhibits phylogeographic structure suggesting that these frogs are naturally-occurring on the islands of Sumbawa, Sumba, Flores, and likely others as well.

Eutropis multifasciata populations on Bali, Pantar, and Wetar are each monophyletic suggesting isolation on those islands, whereas Lombok, Sumbawa, Flores, Sumba, and Alor share either a common haplotype or very closely related haplotypes suggesting either recent or continued movement between those islands. *Eutropis multifasciata* has likely occurred in the Lesser Sundas for a significant amount of time but it is unclear if they have been moved between islands by people or if they are such prolific natural dispersers that they remain genetically unstructured. Future sampling of both genes and localities throughout their range will certainly shed light on this unresolved question.

4.3 | Candidates for human-mediated introduction and dispersal

There is low phylogeographic structure within *P. leucomystax* from the Lesser Sundas and one common haplotype is found throughout the Lesser Sundas, as well as on Java and Bali. The extremely low nucleotide diversity (0.0002) suggests a recent and rapid spread through the Lesser Sundas. Though not yet proven, it has long been suspected that *P. leucomystax* has been moved around much of Southeast Asia by people. Our findings support the hypotheses that *P. leucomystax* has either been recently introduced into and throughout the Lesser Sundas Archipelago or that it has naturally invaded the archipelago very recently followed by rapid colonization of nearly every major island.

Analyses of the snake fauna within the Lesser Sundas suggest that the archipelago's long-standing isolation from other islands in the region have influenced both their species composition and levels of variation between island populations (How & Kitchener, 1997). However, we find that both species of *Lycodon* wolf snakes have very little genetic diversity, no phylogeographical structure, and negative Tajima's D values, suggesting that they have recently expanded their ranges and population sizes as they colonized the islands. *Lycodon capucinus* from the Lesser Sundas are nearly genetically identical to those from the Malay Peninsula suggesting they were recently introduced by humans, and likely continue to be moved between islands. *Lycodon subcinctus* also exhibits minimal genetic diversity suggesting a recent and rapid spread through the archipelago and/or continued movement between islands. However, the lack of *L. subcinctus*

sampling from the nearby Sunda Shelf islands of Java and Bali, as well as the monophyly of Lesser Sundas samples prevent us from ruling out a natural introduction.

4.4 | *Candidate for multiple human-mediated introductions and dispersals*

Movement of reptiles between islands in the Lesser Sundas is certainly known for some species such as the geckos *Hemidactylus frenatus*, *H. platyurus*, and *Gehyra mutilata*, which are commonly seen on ferry boats travelling between islands (pers. obs. S. Reilly). This may be the case for *G. gecko* as well, which has more genetic diversity than the three snakes examined but no discernable phylogeographic structure. *ND4* sequence data for *G. gecko* outside the Lesser Sundas is sparse which prevents the inference of the source populations for the Lesser Sundas. *Gekko gecko* samples within the Lesser Sundas are rendered paraphyletic and nested within samples from China suggesting multiple human mediated introductions. The introduction of the Chinese turtle, *Mauremys reevesii*, to Timor is evidence of the long history of travel and movement of animals between China and Indonesia (Yuwono, 1998; Kaiser *et al.*, 2010). *Gekko gecko* are common in dense human settlements in the region and are known to prey on smaller geckos (such as *Hemidactylus*, *Lepidodactylus*, and *Gehyra*), which are common on boats travelling between islands (Aowphol *et al.*, 2006). Thus, it would not be surprising if *G. gecko* occasionally or routinely stows away on these boats and is thereby moved between islands.

4.5 | *Conservation implications*

Plants and animals have been moved between islands and introduced to new islands, both purposefully and unintentionally, within the Indo-Australian archipelago for thousands of years (Heinsohn, 2003). Certainly, the introduction of some species results in greater ecological change than others, and special caution should be given to prevent the human-mediated spread of those species that could cause major damage such as toxic species (e.g. toads) or certain predators that can devastate naïve native species. For example, the nearby Christmas Island has been heavily impacted by the human-mediated introduction of *L. capucinus*, which has likely caused the extinction of four species of lizards endemic to the island (Smith *et al.*, 2012). The detection of human-mediated introductions of ecologically harmful species will depend on accurate surveys of each island's fauna both in the past (to determine a baseline) and the present

(to detect introductions), and as such we recommend that comprehensive faunal surveys of the Lesser Sundas continue.

5 | CONCLUSIONS

The results from this study show that none of these seven taxa exhibit deep genetic structure as seen in old, naturally occurring taxa such as *Limnonectes* fanged frogs, *Draco* flying lizards, and *Sphenomorphus* forest skinks (Reilly, 2016; Reilly *et al.*, 2019). In light of these results, we cannot definitively reject the hypothesis of human-mediated introductions and/or movements throughout the archipelago for these seven species. For some of these species (*K. baleata*, *E. multifasciata*, *T. insularis*, and *L. subcinctus*), longer term natural introductions remain a viable possibility that requires further investigation, whereas for others (*P. leucomystax*, *G. gecko*, *L. capucinus*) natural introductions seem unlikely in light of these new results, what we know about well-documented introductions elsewhere (such as for *L. capucinus*), and the biology of the species (rampant overwater dispersal over a short temporal extent would be quite unexpected for amphibians). While we have not definitively answered the question of the mode of introduction for most of these taxa, our data clearly indicate that each of these taxa is a relatively recent arrival to the Lesser Sundas Archipelago. We have shed light on the biogeography of each of these taxa and set the stage for others to follow-up with more comprehensive sampling of localities and genes.

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ORCID

Sean B. Reilly - <http://orcid.org/0000-0003-1661-0543>

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TABLE 1 Mitochondrial marker information. bp= base pairs; n=number of samples;
LS=includes only samples from Lesser Sundas.

Species	gene	bp	seq. evol. model	n (LS)	# LS Islands Sampled	LS Variable Sites	LS Parsimony Inf. Sites
<i>Kaloula baleata</i>	<i>16S</i>	831	GTR	13	4	22	10
<i>Polypedates leucomystax</i>	<i>16S</i>	892	HKY+I	41	5	4	0
<i>Eutropis multifasciata</i>	<i>ND4</i>	892	HKY+I	36	8	54	10
<i>Gekko gecko</i>	<i>ND4</i>	840	HKY	34	10	17	11
<i>Lycodon capucinus</i>	<i>cytb</i>	1,073	GTR+I	19	8	2	1
<i>Lycodon subcinctus</i>	<i>cytb</i>	1,078	GTR+I	8	5	1	0
<i>Trimeresurus insularis</i>	<i>ND4+cytb</i>	1,974	HKY+I	57	9	10	2

TABLE 2 Mitochondrial marker summary statistics and divergence times. h= haplotype diversity, π = nucleotide diversity; MRCA= most recent common ancestor; Ma= millions of years ago; *= statistically significant.

Species	h	π	Tajima's <i>D</i>	Fu's <i>F_s</i>
<i>Kaloula baleata</i>	-	-	-	-
- "Java/Bali/Timor" clade	0.60	0.0031	-1.37 (P>0.10)	1.02
- "Lesser Sundas" clade	0.83	0.0037	-0.58 (P>0.10)	-0.85
<i>Polypedates leucomystax</i>	0.10	0.0002	-1.49 (P>0.10)	-2.66
<i>Eutropis multifasciata</i>	-	-	-	-
- "Bali/Timor" clade	0.87	0.0117	-0.39 (P>0.10)	2.55
- "Lesser Sundas" clade	0.91	0.0024	-2.20 (P<0.01)*	-16.52
<i>Gekko gecko</i>	0.72	0.0044	-0.77 (P>0.10)	-0.81
<i>Lycodon capucinus</i>	0.29	0.0003	-1.12 (P>0.10)	-1.15
<i>Lycodon subcinctus</i>	0.25	0.0002	-1.05 (P>0.10)	-0.18
<i>Trimeresurus insularis</i>	0.47	0.0006	-1.36 (P>0.10)	-5.19

FIGURE 1

Frogs

Lizards

Snakes

FIGURE 2

576

577 **FIGURE 3**

578

579 **FIGURE 3 cont.**

FIGURE LEGENDS

FIGURE 1 Map of the Sunda Shelf and Wallacea regions with the borders of the Sunda Shelf shown as a yellow line and the border of the Sahul Shelf shown as a red line. Wallacea consists of the oceanic islands between those two shelves.

FIGURE 2 A-G. Photos of focal taxa and their geographic range within Southeast Asia. -A. *Kaloula baleata*, -B. *Polypedates leucomystax*, -C. *Eutropis multifasciata*, -D. *Gekko gecko*, -E. *Lycodon capucinus*, -F. *Lycodon subcinctus*, and -G. *Trimeresurus insularis*.

FIGURE 3 A-G. Maximum Likelihood phylogenies and represented islands. Each box contains a map of the Lesser Sundas region (including Bali and Nusa Penida) with sampled islands color filled. Unsourced islands where the species is known to occur are shaded light grey. Numbers at nodes represent bootstrap support. Text in boxes represents most recent common ancestor (MRCA) age estimates for relevant lineages. The numbers alongside islands in box A and E correspond to relevant islands: 1-Bali, 2-Nusa Penida, 3-Lombok, 4-Sumbawa, 5-Komodo, 6-Flores, 7-Adonara, 8-Lembata, 9-Pantar, 10-Alor, 11-Wetar, 12-Timor, 13-Rote, 14-Sabu, 15-Sumba.

SUPPLEMENTAL MATERIAL

TABLE S1 Dates of the first records of each species on major islands in the Lesser Sundas.

Numbers in brackets correspond to the supplemental literature cited below*.

Species	Bali	Lombok	Sumbawa	Sumba	Komodo	Flores	Lembata	Alor	Wetar	Savu	Rote	Timor
<i>Kaloula baleata</i>	1927 [1]	1927 [1]	1927 [1]	1897 [5]	1927 [1]	1927 [1]	2011 [7]					2009 [7]
<i>Polypedates leucomystax</i>	1927 [1]	1907 [6]	1927 [1]	1897 [5]		1927 [1]						1923 [3]
<i>Eutropis multifasciatus</i>	1927 [1]	1897 [5]	1917 [2]		1927 [1]	1917 [2]		1917 [2]	1917 [2]			1917 [2]
<i>Gekko gekko</i>	1927 [1]	1897 [5]	1927 [1]	1917 [2]	1927 [1]	1917 [2]		1917 [2]		1897 [5]	1898 [4]	1898 [4]
<i>Lycodon capucinus</i>	1917 [2]		1917 [2]	1897 [5]	1927 [1]	1917 [2]	1917 [2]	1917 [2]	1917 [2]	1897 [5]	1898 [4]	1917 [2]
<i>Lycodon subcinctus</i>		1897 [5]	1917 [2]			1958 [8]						
<i>Trimeresurus insularis</i>		1927 [1]	1927 [1]		1927 [1]	1927 [1]					1898 [4]	1898 [4]

*Supplemental Literature

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623 **TABLE S2** Museum numbers and locality information for samples used in this study.

Museum #	Field Catalog #	Species	Island	Latitude	Longitude
MVZ274408	ALS27	<i>Eutropis multifasciata</i>	Bali	-8.43810	115.40172
MVZ274409	ALS28	<i>Eutropis multifasciata</i>	Bali	-8.43810	115.40172
MVZ274410	ALS29	<i>Eutropis multifasciata</i>	Bali	-8.43810	115.40172
MVZ274411	ALS45	<i>Eutropis multifasciata</i>	Bali	-8.43810	115.40172
MVZ274412	ALS46	<i>Eutropis multifasciata</i>	Bali	-8.43810	115.40172
MVZ291606	JAM11532	<i>Eutropis multifasciata</i>	Lombok	-8.52854	116.28206
MVZ291607	JAM11610	<i>Eutropis multifasciata</i>	Lombok	-8.53159	116.39878
MVZ291608	JAM11709	<i>Eutropis multifasciata</i>	Sumbawa	-8.41016	117.21491
MVZ291609	JAM11767	<i>Eutropis multifasciata</i>	Sumbawa	-8.73561	117.73106
MVZ291610	JAM11782	<i>Eutropis multifasciata</i>	Flores	-8.54530	119.91059
MVZ291611	JAM11783	<i>Eutropis multifasciata</i>	Flores	-8.54530	119.91059
MVZ291612	JAM11898	<i>Eutropis multifasciata</i>	Lombok	-8.53912	116.53959
MVZ291613	JAM11899	<i>Eutropis multifasciata</i>	Lombok	-8.53912	116.53959
MVZ291614	JAM11900	<i>Eutropis multifasciata</i>	Lombok	-8.53912	116.53959
MVZ291615	JAM11901	<i>Eutropis multifasciata</i>	Lombok	-8.53912	116.53959
MVZ291616	JAM11922	<i>Eutropis multifasciata</i>	Lombok	-8.36115	116.52200
MVZ291617	JAM11923	<i>Eutropis multifasciata</i>	Lombok	-8.36115	116.52200
MVZ291618	JAM11924	<i>Eutropis multifasciata</i>	Lombok	-8.36115	116.52200
MVZ291619	JAM11944	<i>Eutropis multifasciata</i>	Lombok	-8.36115	116.52200
MVZ291620	JAM12014	<i>Eutropis multifasciata</i>	Lombok	-8.36115	116.52000
MVZ291621	JAM12108	<i>Eutropis multifasciata</i>	Sumbawa	-8.91228	116.75224
MVZ291622	JAM12109	<i>Eutropis multifasciata</i>	Sumbawa	-8.51717	118.31950
MVZ291623	JAM12110	<i>Eutropis multifasciata</i>	Sumbawa	-8.51717	118.31950
MVZ291624	JAM12174	<i>Eutropis multifasciata</i>	Sumbawa	-8.54700	118.46947
MVZ291625	JAM12175	<i>Eutropis multifasciata</i>	Sumbawa	-8.54700	118.46947
MVZ291626	JAM12202	<i>Eutropis multifasciata</i>	Sumbawa	-8.67775	118.68163
MVZ291627	JAM12305	<i>Eutropis multifasciata</i>	Sumbawa	-8.76643	118.60496
MVZ291628	JAM12324	<i>Eutropis multifasciata</i>	Sumbawa	-8.76296	118.61102
MVZ291629	JAM12340	<i>Eutropis multifasciata</i>	Sumbawa	-8.59961	119.01229
MVZ291630	JAM12341	<i>Eutropis multifasciata</i>	Sumbawa	-8.59961	119.01229
MVZ291631	JAM12342	<i>Eutropis multifasciata</i>	Sumbawa	-8.59961	119.01229
MVZ291632	JAM13006	<i>Eutropis multifasciata</i>	Alor	-8.17922	124.55897
MVZ291633	JAM13007	<i>Eutropis multifasciata</i>	Alor	-8.17922	124.55897
MVZ291634	JAM13137	<i>Eutropis multifasciata</i>	Sumba	-10.02102	120.05795
MVZ291635	JAM13159	<i>Eutropis multifasciata</i>	Sumba	-10.02102	120.05795
MVZ291636	JAM13822	<i>Eutropis multifasciata</i>	Wetar	-7.92789	126.40831
MVZ291637	JAM13830	<i>Eutropis multifasciata</i>	Wetar	-7.92235	126.40569
MVZ291638	JAM13896	<i>Eutropis multifasciata</i>	Wetar	-7.91965	126.39785
MVZ291639	JAM14016	<i>Eutropis multifasciata</i>	Pantar	-8.35268	124.25156
MVZ291640	JAM14062	<i>Eutropis multifasciata</i>	Pantar	-8.35392	124.25345
MVZ291641	JAM13626	<i>Eutropis multifasciata</i>	Timor	-10.03848	123.93333
MVZ274447	ALS43	<i>Gekko gekko</i>	Bali	-8.43810	115.40172
MVZ274448	ALS44	<i>Gekko gekko</i>	Bali	-8.43810	115.40172
MVZ291642	SBR113	<i>Gekko gekko</i>	Rote	-10.88656	122.82613

625 **TABLE S2 cont.**

Museum #	Field Catalog #	Species	Island	Latitude	Longitude
MVZ291643	JAM11612	<i>Gekko gekko</i>	Lombok	-8.58987	116.12589
MVZ291644	JAM11765	<i>Gekko gekko</i>	Sumbawa	-8.67102	118.23570
MVZ291645	JAM11896	<i>Gekko gekko</i>	Bali	-8.81452	115.10137
MVZ291646	JAM12038	<i>Gekko gekko</i>	Sumbawa	-9.02763	116.81893
MVZ291647	JAM12039	<i>Gekko gekko</i>	Sumbawa	-9.02763	116.81893
MVZ291648	JAM12088	<i>Gekko gekko</i>	Sumbawa	-8.76137	118.00056
MVZ291649	JAM12096	<i>Gekko gekko</i>	Sumbawa	-8.60250	118.28671
MVZ291650	JAM12117	<i>Gekko gekko</i>	Sumbawa	-8.43721	118.30004
MVZ291651	JAM12194	<i>Gekko gekko</i>	Sumbawa	-8.51728	118.31947
MVZ291652	JAM12255	<i>Gekko gekko</i>	Sumbawa	-8.49715	118.80463
MVZ291653	JAM12301	<i>Gekko gekko</i>	Sumbawa	-8.50065	119.03625
MVZ291654	JAM12369	<i>Gekko gekko</i>	Flores	-8.78828	121.67159
MVZ291655	JAM12370	<i>Gekko gekko</i>	Flores	-8.78828	121.67159
MVZ291656	JAM12371	<i>Gekko gekko</i>	Flores	-8.78828	121.67159
MVZ291657	JAM12413	<i>Gekko gekko</i>	Flores	-8.54537	119.91075
MVZ291658	JAM12539	<i>Gekko gekko</i>	Flores	-8.61050	122.39379
MVZ291659	JAM12954	<i>Gekko gekko</i>	Alor	-8.16476	124.74838
MVZ291660	JAM12989	<i>Gekko gekko</i>	Alor	-8.18862	124.75208
MVZ291661	JAM12990	<i>Gekko gekko</i>	Alor	-8.19025	124.75142
MVZ291662	JAM12991	<i>Gekko gekko</i>	Alor	-8.19025	124.75142
MVZ291663	JAM12992	<i>Gekko gekko</i>	Alor	-8.19025	124.75142
MVZ291664	JAM13026	<i>Gekko gekko</i>	Flores	-8.21648	122.97288
MVZ291665	JAM13169	<i>Gekko gekko</i>	Sumba	-10.01944	120.05637
MVZ291666	JAM13416	<i>Gekko gekko</i>	Sabu	-10.50747	121.99487
MVZ291667	JAM13548	<i>Gekko gekko</i>	Timor	-10.02225	123.86884
MVZ291668	JAM13560	<i>Gekko gekko</i>	Timor	-10.10636	123.71033
MVZ291669	JAM13575	<i>Gekko gekko</i>	Timor	-10.02339	123.86659
MVZ291670	JAM13588	<i>Gekko gekko</i>	Timor	-10.03903	123.93174
MVZ291671	JAM13654	<i>Gekko gekko</i>	Wetar	-7.93010	126.41180
MVZ291672	JAM13701	<i>Gekko gekko</i>	Wetar	-7.92621	126.40793
MVZ291673	JAM13714	<i>Gekko gekko</i>	Wetar	-7.92686	126.41972
MVZ291674	JAM13873	<i>Gekko gekko</i>	Wetar	-7.92237	126.40568
MVZ291675	JAM13940	<i>Gekko gekko</i>	Pantar	-8.35555	124.25712
MVZ291676	JAM13941	<i>Gekko gekko</i>	Pantar	-8.35555	124.25712
MVZ291677	JAM14089	<i>Gekko gekko</i>	Nusa Penida	-8.68072	115.48843
MVZ291190	JAM11945	<i>Trimeresurus insularis</i>	Lombok	-8.25729	116.44359
MVZ291191	JAM11946	<i>Trimeresurus insularis</i>	Lombok	-8.30545	116.40701
MVZ291192	JAM12005	<i>Trimeresurus insularis</i>	Lombok	-8.30634	116.40496
MVZ291193	JAM12031	<i>Trimeresurus insularis</i>	Sumbawa	-9.00542	116.75720
MVZ291194	JAM12057	<i>Trimeresurus insularis</i>	Sumbawa	-9.05051	116.86373
MVZ291195	JAM12076	<i>Trimeresurus insularis</i>	Sumbawa	-9.00639	116.76723
MVZ291196	JAM12171	<i>Trimeresurus insularis</i>	Sumbawa	-8.66990	118.43940
MVZ291197	JAM12209	<i>Trimeresurus insularis</i>	Sumbawa	-8.74106	118.60437
MVZ291198	JAM12227	<i>Trimeresurus insularis</i>	Sumbawa	-8.71271	118.62209

627 **TABLE S2 cont.**

Museum #	Field Catalog #	Species	Island	Latitude	Longitude
MVZ291199	JAM12228	<i>Trimeresurus insularis</i>	Sumbawa	-8.54886	118.40537
MVZ291200	JAM12262	<i>Trimeresurus insularis</i>	Sumbawa	-8.65415	118.09328
MVZ291201	JAM12303	<i>Trimeresurus insularis</i>	Sumbawa	-8.57221	118.87612
MVZ291202	JAM12320	<i>Trimeresurus insularis</i>	Sumbawa	-8.76643	118.60496
MVZ291203	JAM12332	<i>Trimeresurus insularis</i>	Sumbawa	-8.76300	118.60707
MVZ291204	JAM12482	<i>Trimeresurus insularis</i>	Flores	-8.68687	121.03889
MVZ291205	JAM12483	<i>Trimeresurus insularis</i>	Flores	-8.68687	121.03889
MVZ291206	JAM12484	<i>Trimeresurus insularis</i>	Flores	-8.68687	121.03889
MVZ291207	JAM12485	<i>Trimeresurus insularis</i>	Flores	-8.68687	121.03889
MVZ291208	JAM12524	<i>Trimeresurus insularis</i>	Flores	-8.75954	121.70090
MVZ291209	JAM12525	<i>Trimeresurus insularis</i>	Flores	-8.75954	121.70090
MVZ291210	JAM12541	<i>Trimeresurus insularis</i>	Flores	-8.54421	122.51745
MVZ291211	JAM12543	<i>Trimeresurus insularis</i>	Flores	-8.49705	122.54664
MVZ291212	JAM12544	<i>Trimeresurus insularis</i>	Flores	-8.41902	122.81760
MVZ291213	JAM12549	<i>Trimeresurus insularis</i>	Flores	-8.48070	122.58190
MVZ291214	JAM12550	<i>Trimeresurus insularis</i>	Flores	-8.48936	122.60113
MVZ291215	JAM12551	<i>Trimeresurus insularis</i>	Flores	-8.49313	122.60400
MVZ291216	JAM12552	<i>Trimeresurus insularis</i>	Flores	-8.50030	122.76844
MVZ291217	JAM12553	<i>Trimeresurus insularis</i>	Flores	-8.41956	122.81806
MVZ291218	JAM12749	<i>Trimeresurus insularis</i>	Lembata	-8.38181	123.40195
MVZ291219	JAM12799	<i>Trimeresurus insularis</i>	Lembata	-8.38181	123.40195
MVZ291220	JAM12882	<i>Trimeresurus insularis</i>	Alor	-8.18880	124.69309
MVZ291221	JAM13053	<i>Trimeresurus insularis</i>	Flores	-8.68277	122.21175
MVZ291222	JAM13082	<i>Trimeresurus insularis</i>	Sumba	-10.01906	120.05923
MVZ291223	JAM13152	<i>Trimeresurus insularis</i>	Sumba	-10.02426	120.05718
MVZ291224	JAM13153	<i>Trimeresurus insularis</i>	Sumba	-10.02426	120.05718
MVZ291227	JAM13189	<i>Trimeresurus insularis</i>	Sumba	-10.02012	120.05795
MVZ291228	JAM13255	<i>Trimeresurus insularis</i>	Sumba	-10.02193	120.05812
MVZ291229	JAM13551	<i>Trimeresurus insularis</i>	Timor	-10.02225	123.86884
MVZ291230	JAM13552	<i>Trimeresurus insularis</i>	Timor	-10.02225	123.86884
MVZ291231	JAM13553	<i>Trimeresurus insularis</i>	Timor	-10.02225	123.86884
MVZ291232	JAM13554	<i>Trimeresurus insularis</i>	Timor	-10.02225	123.86884
MVZ291233	JAM13555	<i>Trimeresurus insularis</i>	Timor	-10.02225	123.86884
MVZ291234	JAM13556	<i>Trimeresurus insularis</i>	Timor	-10.02225	123.86884
MVZ291235	JAM13597	<i>Trimeresurus insularis</i>	Timor	-10.03903	123.93174
MVZ291236	JAM13696	<i>Trimeresurus insularis</i>	Wetar	-7.92847	126.40781
MVZ291237	JAM13697	<i>Trimeresurus insularis</i>	Wetar	-7.92769	126.40819
MVZ291238	JAM13698	<i>Trimeresurus insularis</i>	Wetar	-7.92981	126.40920
MVZ291239	JAM13715	<i>Trimeresurus insularis</i>	Wetar	-7.92686	126.41972
MVZ291241	JAM13781	<i>Trimeresurus insularis</i>	Wetar	-7.92599	126.40797
MVZ291244	JAM13885	<i>Trimeresurus insularis</i>	Wetar	-7.92853	126.40974
MVZ291245	JAM13886	<i>Trimeresurus insularis</i>	Wetar	-7.92225	126.40114
MVZ291246	JAM13970	<i>Trimeresurus insularis</i>	Pantar	-8.35124	124.25074
MVZ291247	JAM14035	<i>Trimeresurus insularis</i>	Pantar	-8.35392	124.25347

630 **TABLE S2 cont.**

Museum #	Field Catalog #	Species	Island	Latitude	Longitude
MVZ291248	JAM14036	<i>Trimeresurus insularis</i>	Pantar	-8.35392	124.25347
MVZ291249	SBR216	<i>Trimeresurus insularis</i>	Timor	-9.82180	124.31034
MVZ291250	SBR217	<i>Trimeresurus insularis</i>	Timor	-9.82180	124.31034
MVZ291251	SBR218	<i>Trimeresurus insularis</i>	Timor	-9.82180	124.31034
MVZ291678	JAM11562	<i>Lycodon subcinctus</i>	Lombok	-8.54447	116.39862
MVZ291679	JAM11707	<i>Lycodon subcinctus</i>	Sumbawa	-8.57435	117.31339
MVZ291680	JAM12224	<i>Lycodon subcinctus</i>	Sumbawa	-8.73993	118.60497
MVZ291681	JAM12414	<i>Lycodon subcinctus</i>	Flores	-8.59420	119.96857
MVZ291682	JAM12554	<i>Lycodon subcinctus</i>	Flores	-8.40184	122.84223
MVZ291683	JAM13037	<i>Lycodon subcinctus</i>	Flores	-8.23836	122.97288
MVZ291684	JAM12747	<i>Lycodon subcinctus</i>	Lembata	-8.38181	123.40195
MVZ291685	JAM14037	<i>Lycodon subcinctus</i>	Pantar	-8.35392	124.25347
MVZ273765	ALS86	<i>Lycodon capucinus</i>	Bali	-8.82545	115.09189
MVZ291686	JAM11766	<i>Lycodon capucinus</i>	Sumbawa	-8.66042	118.08301
MVZ291687	JAM12095	<i>Lycodon capucinus</i>	Sumbawa	-8.66243	118.26863
MVZ291688	JAM12263	<i>Lycodon capucinus</i>	Sumbawa	-8.65627	118.08421
MVZ291689	JAM12270	<i>Lycodon capucinus</i>	Sumbawa	-8.48579	118.78094
MVZ291690	JAM12537	<i>Lycodon capucinus</i>	Flores	-8.61050	122.39379
MVZ291691	JAM12538	<i>Lycodon capucinus</i>	Flores	-8.61061	122.39728
MVZ291692	JAM12540	<i>Lycodon capucinus</i>	Flores	-8.57409	122.39379
MVZ291693	JAM12542	<i>Lycodon capucinus</i>	Flores	-8.49705	122.54664
MVZ291694	JAM13971	<i>Lycodon capucinus</i>	Pantar	-8.35268	124.25156
MVZ291695	JAM14049	<i>Lycodon capucinus</i>	Pantar	-8.35591	124.25462
MVZ291696	JAM12918	<i>Lycodon capucinus</i>	Alor	-8.16564	124.74774
MVZ291697	JAM13916	<i>Lycodon capucinus</i>	Wetar	-7.92478	126.40736
MVZ291698	JAM13338	<i>Lycodon capucinus</i>	Sabu	-10.51187	121.98785
MVZ291699	JAM13339	<i>Lycodon capucinus</i>	Sabu	-10.51187	121.98785
MVZ291700	JAM13404	<i>Lycodon capucinus</i>	Sabu	-10.50038	121.98094
MVZ291701	SBR192	<i>Lycodon capucinus</i>	Rote	-10.74501	123.05447
MVZ291702	JAM13576	<i>Lycodon capucinus</i>	Timor	-10.02945	123.36151
MVZ291703	JAM13633	<i>Lycodon capucinus</i>	Timor	-10.26607	123.56586
MVZ291704	JAM13634	<i>Lycodon capucinus</i>	Timor	-10.26607	123.56586
-	Christmas Is. 1	<i>Lycodon capucinus</i>	Christmas Island	-10.48775	105.64536
-	Christmas Is. 2	<i>Lycodon capucinus</i>	Christmas Island	-10.48775	105.64536
-	Christmas Is. 3	<i>Lycodon capucinus</i>	Christmas Island	-10.48775	105.64536
-	Christmas Is. 4	<i>Lycodon capucinus</i>	Christmas Island	-10.48775	105.64536
-	Christmas Is. 5	<i>Lycodon capucinus</i>	Christmas Island	-10.48775	105.64536
MVZ291705	JAM11727	<i>Kaloula baleata</i>	Sumbawa	-8.72371	117.38319
MVZ291706	JAM11728	<i>Kaloula baleata</i>	Sumbawa	-8.72371	117.38319
MVZ291707	JAM11729	<i>Kaloula baleata</i>	Sumbawa	-8.72371	117.38319
MVZ291708	JAM13028	<i>Kaloula baleata</i>	Flores	-8.21648	122.97288
MVZ291709	JAM13058	<i>Kaloula baleata</i>	Sumba	-9.82975	119.92864
MVZ291710	JAM13081	<i>Kaloula baleata</i>	Sumba	-10.02102	120.05795
MVZ291711	JAM13259	<i>Kaloula baleata</i>	Sumba	-10.01994	120.05637

632 **TABLE S2 cont.**

Museum #	Field Catalog #	Species	Island	Latitude	Longitude
MVZ291712	JAM13499	<i>Kaloula baleata</i>	Timor	-10.24424	123.65848
MVZ291713	JAM13500	<i>Kaloula baleata</i>	Timor	-10.24424	123.65848
MVZ291714	JAM13501	<i>Kaloula baleata</i>	Timor	-10.24424	123.65848
MVZ291715	JAM13502	<i>Kaloula baleata</i>	Timor	-10.24424	123.65848
MVZ273785	ALS13	<i>Polypedates leucomystax</i>	Bali	-8.82545	115.09189
MVZ273786	ALS14	<i>Polypedates leucomystax</i>	Bali	-8.82545	115.09189
MVZ273787	ALS19	<i>Polypedates leucomystax</i>	Bali	-8.82545	115.09189
MVZ273788	ALS20	<i>Polypedates leucomystax</i>	Bali	-8.82545	115.09189
MVZ273781	ALS60	<i>Polypedates leucomystax</i>	Bali	-8.43810	115.40172
MVZ273782	ALS61	<i>Polypedates leucomystax</i>	Bali	-8.43810	115.40172
MVZ273783	ALS62	<i>Polypedates leucomystax</i>	Bali	-8.43810	115.40172
MVZ291716	SBR214	<i>Polypedates leucomystax</i>	Timor	-9.82180	124.31039
MVZ291717	JAM11595	<i>Polypedates leucomystax</i>	Lombok	-8.53159	116.39878
MVZ291718	JAM11721	<i>Polypedates leucomystax</i>	Sumbawa	-8.75751	117.34994
MVZ291719	JAM11763	<i>Polypedates leucomystax</i>	Sumbawa	-8.52740	118.31392
MVZ291720	JAM11764	<i>Polypedates leucomystax</i>	Sumbawa	-8.52740	118.31392
MVZ291721	JAM11897	<i>Polypedates leucomystax</i>	Bali	-8.81452	115.10137
MVZ291722	JAM11998	<i>Polypedates leucomystax</i>	Lombok	-8.30782	116.40483
MVZ291723	JAM11999	<i>Polypedates leucomystax</i>	Lombok	-8.30782	116.40483
MVZ291724	JAM12221	<i>Polypedates leucomystax</i>	Sumbawa	-8.73993	118.60497
MVZ291725	JAM12222	<i>Polypedates leucomystax</i>	Sumbawa	-8.73993	118.60497
MVZ291726	JAM12223	<i>Polypedates leucomystax</i>	Sumbawa	-8.73993	118.60497
MVZ291727	JAM12294	<i>Polypedates leucomystax</i>	Sumbawa	-8.50065	119.03625
MVZ291728	JAM12307	<i>Polypedates leucomystax</i>	Sumbawa	-8.76643	118.60496
MVZ291729	JAM12491	<i>Polypedates leucomystax</i>	Flores	-8.68687	121.03889
MVZ291730	JAM12492	<i>Polypedates leucomystax</i>	Flores	-8.68687	121.03889
MVZ291731	JAM12493	<i>Polypedates leucomystax</i>	Flores	-8.68687	121.03889
MVZ291732	JAM12494	<i>Polypedates leucomystax</i>	Flores	-8.68687	121.03889
MVZ291733	JAM12495	<i>Polypedates leucomystax</i>	Flores	-8.68687	121.03889
MVZ291734	JAM12496	<i>Polypedates leucomystax</i>	Flores	-8.68687	121.03889
MVZ291735	JAM12497	<i>Polypedates leucomystax</i>	Flores	-8.68687	121.03889
MVZ291736	JAM12498	<i>Polypedates leucomystax</i>	Flores	-8.68687	121.03889
MVZ291737	JAM12499	<i>Polypedates leucomystax</i>	Flores	-8.68687	121.03889
MVZ291738	JAM13027	<i>Polypedates leucomystax</i>	Flores	-8.21648	122.97288
MVZ291739	JAM13055	<i>Polypedates leucomystax</i>	Sumba	-9.82975	119.92864
MVZ291740	JAM13056	<i>Polypedates leucomystax</i>	Sumba	-9.82975	119.92864
MVZ291741	JAM13079	<i>Polypedates leucomystax</i>	Sumba	-10.02102	120.05795
MVZ291742	JAM13080	<i>Polypedates leucomystax</i>	Sumba	-10.02102	120.05795
MVZ291743	JAM13143	<i>Polypedates leucomystax</i>	Sumba	-10.02783	120.05765
MVZ291744	JAM13185	<i>Polypedates leucomystax</i>	Sumba	-10.02323	120.06006
MVZ291745	JAM13186	<i>Polypedates leucomystax</i>	Sumba	-10.02323	120.06006
MVZ291746	JAM13192	<i>Polypedates leucomystax</i>	Sumba	-10.01994	120.05637
MVZ291747	JAM13210	<i>Polypedates leucomystax</i>	Sumba	-10.02323	120.06006
MVZ291748	JAM13248	<i>Polypedates leucomystax</i>	Sumba	-10.00728	120.04520

TABLE S2 cont.

Museum #	Field Catalog #	Species	Island	Latitude	Longitude
MVZ291749	JAM13249	<i>Polypedates leucomystax</i>	Sumba	-10.01994	120.05637
MVZ291750	JAM13254	<i>Polypedates leucomystax</i>	Sumba	-10.02314	120.06021
MVZ291751	JAM13506	<i>Polypedates leucomystax</i>	Timor	-10.24424	123.65848
MVZ291752	JAM13507	<i>Polypedates leucomystax</i>	Timor	-10.24424	123.65848
MVZ291753	JAM13510	<i>Polypedates leucomystax</i>	Timor	-10.24424	123.65848
MVZ291754	JAM13511	<i>Polypedates leucomystax</i>	Timor	-10.24424	123.65848
MVZ291755	JAM13512	<i>Polypedates leucomystax</i>	Timor	-10.24424	123.65848
MVZ291756	JAM14087	<i>Polypedates leucomystax</i>	Nusa Penida	-8.71780	115.52113
MVZ291757	JAM14088	<i>Polypedates leucomystax</i>	Nusa Penida	-8.71780	115.52113
MVZ291758	JAM14111	<i>Polypedates leucomystax</i>	Nusa Penida	-8.73340	115.52335