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Molecular tracing of the geographical origin of captive Asian small-clawed otters in Japan

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Abstract

The international trade of the Asian small-clawed otter (*Aonyx cinereus*) for commercial purposes is prohibited by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix I. However, otter smuggling is still rampant, and Japan is among the important destination countries for captive otters whose origins are ambiguous. Our study aims to investigate the geographic origin(s) of Asian small-clawed otters in exotic animal cafés (EACs), zoos/aquariums in Japan, as well as those seized by Japanese customs, by comparing their mitochondrial DNA sequences with those of wild otters in Thailand—a primary trade hub for these animals. We analyzed 1511 bp mitochondrial sequences, including the complete CytB gene and a partial Control Region, in 33 individuals kept in EACs, 43 individuals from zoos/aquariums, and five from Japanese customs seizures, and compared them with the reference sequences from Thailand and neighboring countries. We detected 12 haplotypes among the captive otters in Japan, and the haplotype network was divided into three major groups. Moreover, certain haplotypes found in EACs and seized individuals were also present in wild otters from the southern region of Thailand, which is a suspected poaching hotspot. While more than half (24 of 43) of captive otters in zoos/aquariums share the same haplotypes with their wild counterparts in Thailand, most haplotypes do not match those found in seized and café individuals. According to CITES

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records, this species has not been imported from Thailand into Japan since 1988. Our findings suggest that most (75%) of seized and captive otters at EACs originated from southern Thailand, likely through illegal trade after this date. Expanding the database of samples from captive otters in Japan and wild otters in their original habitats may help to clarify the trade routes of these animals to the country.

KEYWORDS

Aonyx cinereus, exotic animal cafés, mtDNA, trafficking, wildlife forensics, wildlife trade

1 | INTRODUCTION

Poaching and illegal wildlife trade are among the key drivers of biodiversity loss and biosecurity crises worldwide. The United Nations estimates that illegal wildlife trade generates up to 23 billion USD annually (UNODC, 2020). Illegal wildlife trade has already pushed many species to extinction, e.g., the Javan rhinoceros (*Rhinoceros sondaicus*) in Vietnam (Brook et al., 2014), and continues to endanger many species, such as pangolins (Family: Manidae; Cheng et al., 2017). For instance, 27% of 5420 species of mammals that are currently traded are classified as threatened, based on the IUCN Red List, compared to non-traded species, signifying the role of wildlife trade as a driver of extinction risk (Scheffers et al., 2019). In Asia, the illegal pet trade of pet otters threatens the species' survival and population viability of otters.

Asian small-clawed otters (*Aonyx cinereus*) are widely distributed across South and Southeast Asia in coastal wetland habitats, interior hilly riparian zones, and along watercourses (Chutipong et al., 2014; Sharma et al., 2022). Since 2008, the species has been classified as vulnerable by the International Union for Conservation of Nature Red List of Threatened Species (Wright et al., 2021). The main threats to the viability of its populations are habitat fragmentation and loss, human-otter conflict, rampant poaching, and the international wildlife trade (Gomez et al., 2016; Gomez & Bouhuys, 2017, 2018; Kitade & Naruse, 2018; Prakash et al., 2012; Tantipisanuh et al., 2023). In response to its growing risk of extinction, the Asian small-clawed otter was listed on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 2019, limiting its trade to exceptional circumstances (Wright et al., 2021).

Among the major importers of Asian small-clawed otters is Japan (Kitade & Naruse, 2018), while Thailand and Indonesia appear as the main source countries for illegally traded otters (Gomez et al., 2016; Gomez & Bouhuys, 2017, 2018). Over the last two decades alone, more than 100 Asian small-clawed otters were seized at both Thai and Japanese airports (Kitade & Naruse, 2018). Since the late 2000s, Japan has experienced a boom in consumers' demand for exotic pet otters (Kitade & Naruse, 2018), and the archipelago remains a major importer of wild-caught animals (Nijman, 2010). In addition, 46% of the Japanese zoos/aquariums surveyed admitted to having obtained otters from animal dealers (Kitade & Naruse, 2018). Between 1986 and 2019, 382 live Asian small-clawed otters were imported into Japan for all purposes (Okamoto et al., 2024).

Imports and exports of CITES-listed species in Japan are regulated by the Foreign Exchange and Foreign Trade Law from the Ministry of Economy, Trade and Industry, and the Customs Law by the Ministry of Finance—which bans the import of wild otters, except for individuals bred in captivity (e.g., sanctuary), obtained before August 2019 or for research purposes (Okamoto et al., 2020). After 2020, no otter imports, legal or illegal, have been reported in Japan, except for one import for scientific purposes (Okamoto et al., 2024). The main driver for otter demand in Japan is social media, fed by content from zoos and aquariums, otter/exotic animal cafés, and private owners (Harrington et al., 2019; Kitade & Naruse, 2018; McMillan et al., 2021). Otters, mainly Asian small-clawed otters, are very popular on YouTube and Instagram (Harrington et al., 2019). Since its creation in 2018, one of the main "otter" channels in Japan, showcasing the daily lives of two Asian small-clawed otters, has accumulated over 1.82 million subscribers and several hundred million views (as of March 2024). The channel has an official shop with merchandise derived from their "star otters" and the owner also owns popular otter cafés in Tokyo, Nagoya, and Fukuoka. Otter cafés are part of a wider network of exotic animal cafés (EACs), i.e., facilities where customers can view and/or interact with exotic animals while sometimes consuming food and beverages. EACs are widespread across Asia (and found in Cambodia, Hong Kong, Indonesia, Japan,

China, Philippines, South Korea, Taiwan, Thailand, and Vietnam), but Japan is number one in terms of the number of facilities (McMillan et al., 2021). Animal cafés in Japan started in 2004 and have since increased exponentially in number and diversity of species. As of 2019, Japan counted at least 137 active EACs housing 419 species (Ministry of the Environment of Japan, 2016; Sigaud et al., 2023). The Asian small-clawed otter is one of the most popular mammal species in Japanese EACs (McMillan et al., 2021; Okamoto et al., 2024), exhibited at 12 EACs in seven cities as of July 2022 (Okamoto et al., 2024). Some EACs also sell otters, with prices reaching over 10,000 USD for one individual (Nuwer, 2019). In 2018, at least 85 otters were advertised or recorded for sale in Japan (Kitade & Naruse, 2018). Of these, 46% ($n = 39$) were captive-bred within the country, while 20% ($n = 17$) were imported (with unclear origin), and the rest (34%; $n = 29$) came from an unknown source, as reported by sellers (Kitade & Naruse, 2018).

Biological populations include many different levels of genetic variation, and geographic origin identification relies on the assignment of a sample to a particular population (Ogden & Linacre, 2015). DNA analyses applied to ascertain the geographic origin of seized samples and captive individuals with uncertain sources successfully identified poaching areas and traced illegal trade routes for various wildlife, such as ivory (Wasser et al., 2007, 2022; Zhao et al., 2019), pangolins (*Phataginus* spp. and *Smutsia* spp.) from Africa to Asia (Zhang et al., 2020), seized tiger (*Panthera tigris tigris*) parts in Nepal (Karmacharya et al., 2018), and revealed a long-distance translocation and potential laundering of captive-bred European pond turtles (*Emys orbicularis*) into the illegal trade (Velo-Antón et al., 2021). Such wildlife forensics can lead to the development of valuable tools for conservation. For instance, Zhao et al. (2019) developed an interactive software, *Loxodonta Localizer* (www.loxodontalocalizer.org), to track down the origin of confiscated ivory using available mitochondrial DNA (mtDNA) sequences from African elephants (*Loxodonta* spp.). mtDNA mapping based on partial Control Region sequences was also conducted on Asian small-clawed otters, with samples collected at nine sites in Malaysia and Thailand, resulting in the identification of seven haplotypes (Rosli et al., 2014). In addition to the Control Region sequences, previous phylogeographic studies used the Cytochrome *B* (CytB) gene to elucidate the evolutionary history of otter species (Koepfli et al., 2008; Koepfli & Wayne, 1998; Moretti et al., 2017). Ongoing surveys are being conducted to map the reference DNA of otters in their natural habitats across Thailand. However, no studies have been performed on captive otters in Japan, whose geographic origin remains unclear.

In this study, we used maternally inherited mtDNA CytB gene and partial Control Region sequences to (1) estimate the geographic origin and genetic diversity of captive otters in Japanese EACs, zoos, and aquariums, and individuals seized by airport customs and (2) expand the sequence database of Asian small-clawed otters to help develop conservation plans and maintain the genetic diversity and adaptive potential of the species.

2 | METHODS

2.1 | Sampling and DNA extraction

A total of 85 samples were collected from 81 captive Asian small-clawed otters in Japan. We sampled 43 otters kept in 13 different zoos and aquariums. Specifically, we collected blood from seven otters during regular veterinary health examinations, fecal samples from 36 otters using cotton swabs, and ovarian tissue from four of these otters through remnants of ovaries donated by zoos/aquariums for oocyte preservation in deceased individuals. We obtained saliva samples from 33 individuals kept at five EACs/otter cafés using cotton swabs. In addition, we collected fecal samples from five individuals seized at airport customs due to CITES regulations. We extracted DNA from all 81 individuals using the QIAGEN DNeasy Blood and Tissue Kit (QIAGEN, Hilden, Germany) for blood and tissue samples and the QIAamp DNA Stool Mini Kit (QIAGEN) for fecal samples following the manufacturer's instruction. All EACs and captive facilities agreed to the research application and consent form that clearly stated: "Samples taken from private facilities in Japan will be pooled for the analysis and will never be identified/attributed to individual facilities or owners in any publications or communications developed from this research." The procedures were approved following the ethical guidelines and regulations from the animal research committee of the Wildlife Research Center, Kyoto University (No. WRC-2022-010A).

2.2 | Polymerase chain reaction and sequencing reactions

We amplified DNA samples by polymerase chain reaction (PCR) using CytB and the 5′ hypervariable region of the mtDNA Control Region. We used the reported primers L14120F: 5′-CATGAATCTAACCATGACTAGTGAC-3′ and LcanR4: 5′-CATTAGTCCATCGAGATGTCCC-3′ to amplify a 1709 bp fragment, which includes the complete gene sequences of CytB, tRNA-Thr, and tRNA-Pro, as well as the 5′ end of the Control Region (Coudrat

et al., 2022). For PCR, we used TaKaRa LA Taq with GC Buffer (Takara Bio, Shiga, Japan). PCR mixtures (10 μL) for samples extracted from stomatocytes and ovarian tissue included 1 μL of template DNA solution, 5 μL of 2× GC Buffer I (Takara Bio) l, 400 μM of dNTPs, 0.5 U of TaKaRa LA Taq, and 0.4 μM of each primer. For samples extracted from feces, we used PCR mixtures of 2 μL of template DNA solution and 0.1 μL of T4 gene 32 protein (Nippon Gene, Tokyo, Japan) to reduce PCR inhibition in fecal DNA.

The PCR conditions consisted of an initial denaturation at 95°C for 2 min, followed by 40 cycles of thermal denaturation at 95°C for 30 s, annealing at 58°C for 30 s, and extension at 74°C for 30 s. We completed the final extension at 72°C for 10 min. We confirmed PCR amplification using 1.5% agarose electrophoresis running for 20 min at 100 V with Gel red (Fujifilm Wako Pure Chemical Corporation, Osaka, Japan), and PCR product bands were identified around 1709 bp. We purified PCR products using the High Pure PCR Product Purification Kit (Roche, Basel, Switzerland). We performed sequencing reactions using the BigDye Terminator v3.1 Cycle Sequencing Kit (Thermo Fisher Scientific, New York, USA): 5.0 μL of sample DNA, 2 μL of BigDye, 2 μL of Buffer, and 1 μL of primer (100 μM). The PCR thermal cycling was done with an initial denaturation at 96°C for 1 min, followed by 25 cycles of heat denaturation at 96°C for 10 s, annealing at 50°C for 5 s, and extension reaction at 60°C for 1 min. We performed sequencing reactions for each sample in both directions using forward and reverse primers. Purified PCR products expected as 1709 bp were sent to Fasmac (Atsugi, Japan) for Sanger sequencing in December 2022 and January 2023. All samples examined in this study are listed in Table S1.

2.3 | Geographic origin assignment

We obtained 1511 bp sequences from 1709 bp PCR products because both ends of the amplified sequences were obscured. We determined nucleotide consensus sequences using MEGA10 (Kumar et al., 1994, 2016) using a maximum likelihood (ML) method by aligning sequences obtained using forward and reverse primers. The median-joining method (Bandelt et al., 1999) in Network5 (http://www.fluxus-engineering.com/sharenet.htm: accessed on January 13, 2023) was used to construct a haplotype network. Phylogenetic trees were reconstructed using multiple approaches with *Lutrogale perspicillata* sequences as outgroups. Neighbor-joining and maximum parsimony trees were estimated with PAUP* (Swofford, 2003). A ML tree with 10,000 bootstrap replicates was estimated using the IQ-TREE web server (http://iqtree.cibiv.univie.ac.at/; Trifinopoulos et al., 2016). The TN + F + R2 nucleotide substitution model was estimated as the best-fitted nucleotide substitution model based on Corrected Akaike Information Criterion and Bayesian Information Criterion using the IQ-TREE web server. Phylogenetic trees were edited with FigTree v.1.4.2 (Rambaut et al., 2018). Bayesian phylogeny was reconstructed using MrBayes 3.2.7a (Ronquist et al., 2012) by running two independent Markov chain Monte Carlo with four chains of 20×10^6 generations, sampling every 2000 generations until the average standard deviation of the split frequencies decreased to <0.001. The initial 25% of the samples were discarded as burn-in, and the remaining data were used to calculate the posterior probabilities of the maximum clade credibility. We used Tracer v. 1.7.2 (Rambaut et al., 2018) to ensure that the stationarity and convergence between runs were achieved. Statistical supports for each node were displayed above branches when bootstrap values were >50% and below branches when posterior probability from Bayesian inference was >0.7. The geographic origin was inferred by visual inspection of the phylogenetic clustering comparing sequences from this study with those from previous and ongoing genetic studies in Thailand (Table S2), Peninsular Malaysia, and Singapore (Moretti et al., 2017; Salleh et al., 2017).

We evaluated genetic diversity by measuring haplotype diversity (*Hd*), nucleotide diversity (π), and average number of nucleotide differences (k) within three populations (Zoos/Aquariums, EACs, and custom seizures) using DnaSP 6.12 (http://www.ub.edu/dnasp/; Rozas et al., 2017). Genetic distances between haplotypes were calculated using MEGA10 and measured using the Kimura 2-Parameter model (Table S3).

3 | RESULTS

3.1 | Assigning geographic origins

The 1511 bp mtDNA sequences, encompassing the complete CytB gene to the 5′ part of the control region, were successfully amplified from 81 Asian small-clawed otters. These sequences resulted in 12 haplotypes (Table 1, Table S1, and Figure S1).

DNA obtained from samples in Japan was compared with reference DNA samples of known geographic origins (i.e., Thailand, Peninsular Malaysia, and Singapore). Six of the 12 haplotypes (Hap1, Hap4, Hap5, Hap6, Hap10, and Hap12) found in this study matched those identified from wild otters in Thailand (Table 1, Figure 1). Phylogenetic analyses based on neighbor-joining, ML, maximum parsimony, and Bayesian

TABLE 1 Haplotype determination of Asian small-clawed otters in Japan from (i) otter cafés, (ii) airport customs seizures, and (iii) zoos/aquariums, compared to wild otters in Thailand.

	Japan				
Haplotype	**Otter cafés**	**Seizures**	**Zoos/aquariums**	**Total**	**Haplotype in Thailand**
Hap1			18	18	ACTH08
Hap2			1	1	
Hap3			10	10	
Hap4	3	3	5	11	ACTH11
Hap5	22			22	ACTH05
Hap6			3	3	ACTH01,09
Hap7			4	4	
Hap8			1	1	
Hap9			1	1	
Hap10	3	2		5	ACTH04
Hap11	2			2	
Hap12	3			3	ACTH02,03,18,21,24
Numbers of individuals	33	5	43	81	
Number of haplotypes	5	2	8		
Haplotype diversity	0.5436	0.6000	0.7597		

inference provided congruent phylogenetic relationships among Asian small-clawed otter mtDNA haplotypes by supporting the detection of three major clades (A, B, and C) with moderate bootstrap values and posterior probabilities (Figure 1). In particular, Japanese haplotypes from Clade A, including five (Hap1, Hap4, Hap5, Hap6, Hap12) out of six haplotypes, were clustered with those from southern Thailand, and Clade B, including one (Hap10) out of three haplotypes, was clustered with haplotypes from southernmost Thailand close to Malaysia, Peninsular Malaysia, and Singapore (Moretti et al., 2017). The most divergent Clade C, which included three haplotypes (Hap8, Hap9, and Hap11) from Japan, was clustered with a reported haplotype from Sarawak, Malaysia (Moretti et al., 2017).

3.2 | Haplotype network

The analysis of the median-joining haplotype network supported the closely related grouping of six haplotypes that matched those found in Thailand (Figure 2). The observed grouping in the network analysis was consistent with phylogenetic clustering patterns into three clades. Hap1, Hap2, Hap4, Hap5, Hap6, and Hap12 formed Clade A. Hap3, Hap7, and Hap10 formed Clade B. Hap8, Hap9, and Hap11 formed Clade C. Among the six haplotypes matched with those found in Thailand, Hap10 was highly divergent from the others, while the other five haplotypes differed by approximately two single nucleotide polymorphisms and were centered on Hap1.

3.3 | Genetic diversity indices

The closest genetic distances were observed between Hap1-6, Hap4-5, and Hap5-6 in Clade A (0.000662–0.000663, Table S3). Among the matched haplotypes identified in Thailand, Hap10 had the largest genetic distance from the other five haplotypes (>0.008678) and formed a single phylogenetic clade (Clade B) with Hap3 and Hap7. The genetic distance between Hap3 and Hap7 was smaller (0.002654) and similar to the distance between Hap4 and Hap12 (0.002652), but both Hap3 and Hap7 were somewhat distant from Hap10 (0.005323–0.006662).

We detected higher values of π, *Hd*, and *k* in Asian small-clawed otters sampled in zoos and aquariums compared to EACs (Table 2). Among 33 individuals kept in EACs/otter cafés, we identified five haplotypes (Hap4, Hap5, Hap10, Hap11, and Hap12). Hap4 was also found in three customs-seized individuals and four zoo and aquarium individuals (Table 1, Table S1). Hap10 matched two additional seized individuals. Hap5, Hap11, and Hap12 were identified only in EACs/otter cafés. Among these, Hap5 was the most common haplotype (22 individuals) and was identified in all five cafés surveyed. In addition, seven haplotypes (Hap1, Hap2, Hap3, Hap6, Hap7,

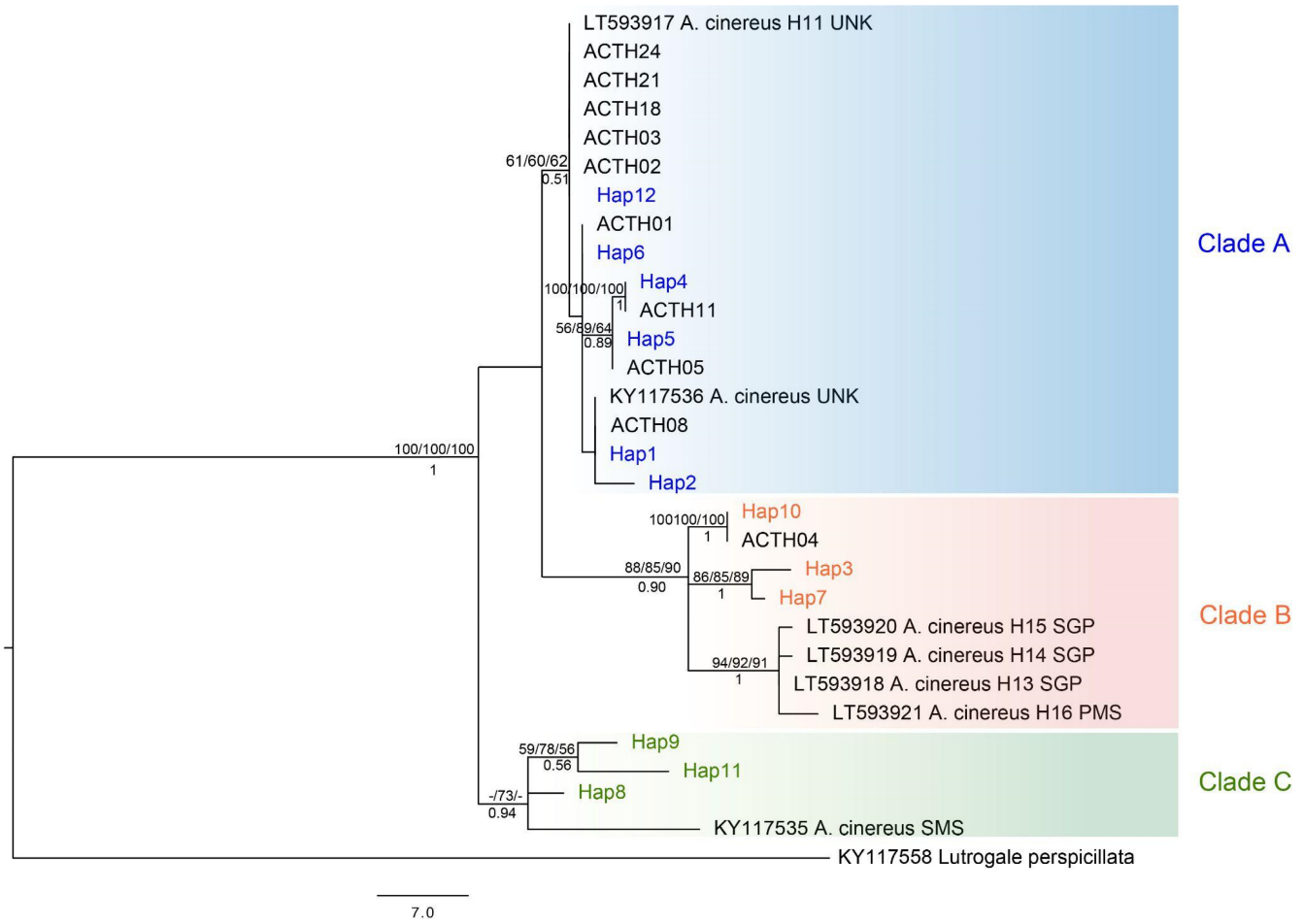

FIGURE 1 Phylogenetic relationships among otter mitochondrial DNA haplotypes based on neighbor-joining method (NJ) and 1511 bp sequences spanning the complete CytB gene and the 5′ part of the Control Region. The sequences were derived from this study, studies from Thailand (ACTH: Table S2: OR361730–OR361739), and other genetic studies in the region (Peninsular Malaysia [PMS], Singapore [SGP], and Sarawak Malaysia [SMS]: Moretti et al., 2017; Salleh et al., 2017). Haplotypes from this study (Hap1–Hap12) are represented in blue alphabet (Clade A), orange alphabet (Clade B), and green alphabet (Clade C). The numbers above branches represent bootstrap support from the NJ/MP/maximum likelihood methods and the below branches are posterior probabilities from Bayesian inference. Smooth-coated otter (*Lutrogale perspicillata*) with Accession Number KY117558 (Salleh et al., 2017) was used as an outgroup.

Hap8, and Hap9) were only found in otters kept at zoos and aquariums.

4 | DISCUSSION

4.1 | Geographic origins

Phylogenetic analyses of a 1511 bp fragment that included the complete CytB and 5′ end of the control region sequenced from three sources of Asian small-clawed otters in Japan show strong bootstrap support for three major clades, possibly corresponding to (i) mainland Indochinese populations (including western and southern Thailand), (ii) Sundaic Population I (including southern Thailand), and (iii) Sundaic Population II (whose countries of origin are currently unknown). Based on the identical haplotypes, most otters (94%) kept at cafés originated from Thailand, compared to around 60% from those kept at zoos and aquariums. The presence of the predominant Hap5—identical to the *A. cinereus* Thailand haplotype ACTH05 found in wild otters in southern Thailand—indicates that the source populations of otters kept in cafés or their maternal lines are potentially from the poaching hotspots encompassing coastal wetlands and hilly riparian areas along the southern Gulf of Thailand. Two haplotypes identified from customs-seized otters (Hap4 and Hap10), which are identical to ACTH11 and ACTH04, respectively, can be traced to hilly riparian areas of the southern west coast of Thailand (Andaman; Hap4) and a possible poaching hotspot in Thailand near the border with Malaysia (Hap10).

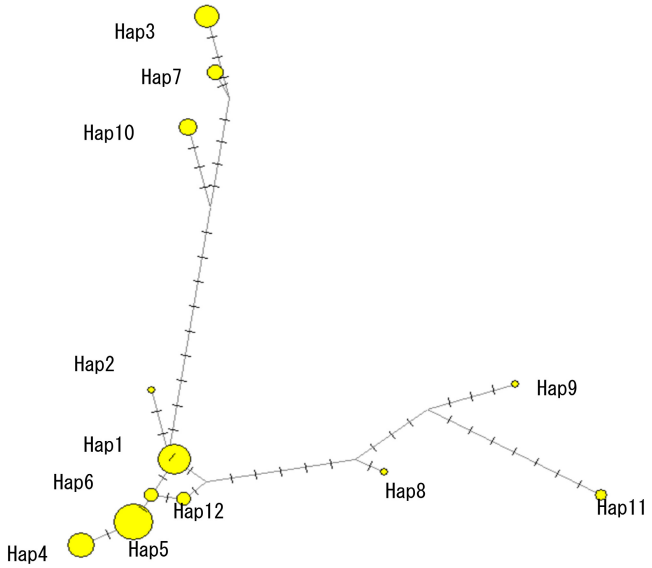

FIGURE 2 Median-joining haplotype network of 12 otter mitochondrial DNA haplotypes from this study based on 1511 bp mtDNA sequences spanning the complete CytB gene and the 5′ part of the Control Region. The size of the circle is proportional to the haplotype frequency. The line length connecting each haplotype is proportional to the nucleotide differences, and the dashed lines represent the number of mutations.

Thailand is a well-recognized source country for otters brought to Japan (Gomez & Bouhuys, 2017). Although many otters are sold at central Thailand markets like the Chatuchak Weekend Market in Bangkok, and seizures usually occur in Bangkok airports (Nishiwaki, 2019; Online Reporters, 2017; Shepherd & Tansom, 2013), our findings indicate that these animals likely originated from the southern parts of the country. Indeed, previous research shows that online sales of Asian small-clawed otters seem targeted to a Thai domestic clientele, and the majority (73%) of sale posts on social media originated from the south of Thailand, especially from provinces directly bordering Malaysia (e.g., Yala; Siriwat and Nijman, 2018). The coastal wetlands of southern Thailand, the Andaman coast in the west and the Gulf of Thailand in the east, and Peninsular Malaysia are vulnerable to poaching (Fernandez, 2018; Kamjing et al., 2022) and may be considered hotspots for illegal wildlife trade. Seizures in Japanese airports have also been reported (Ando, 2019), and the large number of animals (n = 5–12) seized each time likely indicates an organized smuggling operation between Thailand and Japan (Kitade & Naruse, 2018).

Small genetic distance (0.000662), patterns of phylogenetic clustering, and network analysis provided sufficient evidence to infer that most otters currently kept in cafés and from seizures (Hap4, Hap5, Hap10, and Hap12) are likely sourced from one region in Thailand. While Hap12 matched with five haplotypes found in Thailand (Table 1 and Table S2—all from several areas of southern Thailand), it is difficult to pinpoint the exact areas yet. Hap1, Hap5, and Hap10 have been found in geographically adjacent areas in southern Thailand between 9°21′5″N, 98°41′56″E to 9°0′55″N, 99°47′29″E (matched with ACTH08, ACTH05 and ACTH04, respectively, Table S2). Thus, poaching hotspots may exist in areas where individuals with these four haplotypes are present. However, according to the CITES Trade Database (2023), there are no records of otter imports from Thailand to Japan since 1988. This implies that dealers likely acquired the café otters around the time of the pet otter boom (the late 2000s). Although some of the population/founders of cafés and zoos/aquariums possibly came to Japan through dealers before Asian small-clawed otters became listed in CITES Appendix I in 2019, it is unclear where and how the dealers took the otters to Japan. On the other hand, the presence of seven unmatched haplotypes (Hap1, Hap2, Hap3, Hap6, Hap7, Hap8, and Hap9) in otters from zoos and aquariums, EACs/otter cafés, and seizures by airport authorities, despite some overlap, suggests different geographic origins among them. Within the haplotypes only seen in otters from zoos and aquariums, most haplotypes, except Hap1 and Hap6, were not found in the wild habitat in Thailand. The gap in reference haplotype coverage from the wild populations may hinder the determination of the geographic origins of traded otters. While Hap1 is matched with only ACTH08 (the Gulf of Thailand coast between 9°21′5″N, 98°41′56″E to 9°0′55″N, 99°47′29″E), Hap6 matched two Thailand haplotypes (ACTH01 and ACTH09), which were found along the Andaman coast between 6°44′27″N, 99°58′20″E and 7°38′44″N, 99°20′49″E in southern Thailand (Table S2). To distinguish the different sequences shown in ACTH01 and ACTH09 with Japanese samples, longer sequences or complete mitochondrial genomes will be required. The regions of the Hap6 sequences examined in this study have different ranges in the wild.

Of the haplotypes that did not match those in Thailand populations (Hap2, Hap3, Hap7, Hap8, Hap9, and Hap11), Hap2 is close (0.001988) in genetic distance to Hap1, which is comparable to the distance between Hap1 and Hap4 (Thai counterpart ACTH11 found in the Malaysia border). To date, reference sequences from wild otters in Southeast Asia do not match Hap2; therefore, we can only assume that its origin is most likely from other parts of southern Thailand and/or the Malay Peninsula. Alternatively, if the otter population has experienced a drastic decline and become small and isolated, random genetic drift and/or inbreeding could have

TABLE 2 Mitochondrial DNA diversity indices from three captive Asian small-clawed otter groups in Japan: (i) otter cafés, (ii) airport customs seizures, and (iii) zoos/aquariums.

Population	Otter cafés	Seizures	Zoos/aquariums
Number of animals	33	5	43
Haplotype number	5	2	8
Nucleotide diversity (π)	0.00316	0.00635	0.00621
Haplotype diversity (Hd)	0.5436	0.6000	0.7597
Average number of nucleotide differences (k)	4.777	9.600	9.101

resulted in the loss of Hap2 from wild populations. Maintaining the genetic reservoir of this haplotype in captivity is, therefore, crucial for the diversity and adaptive potential of the founders of future genetic exchanges among Asian countries are needed.

Hap3 was identified in one otter brought to Japan from Indonesia. Indonesia is a primary otter exporter with a large domestic market, leading the otter online trade in Southeast Asia (Gomez & Bouhuys, 2018). Since 2010, of 176 Asian small-clawed otters legally imported into Japan, almost half of the animals ($n = 83$) came from Indonesia (CITES Trade Database, 2023). Further genetic identification of Asian small-clawed otters in Indonesia and Malaysia is necessary to estimate the geographic origin of Hap3 and Hap7.

Our inferred three genetic clusters within Asian small-clawed otters are consistent with geographic subdivisions within mammals in Indochinese and Sundaic biogeographic regions. The evolutionary history of our samples in Clade C, which consists of Hap8, Hap9, and Hap11, is closely related to the Sundaic Sarawak populations in the northwest of Borneo Island (Salleh et al., 2017; Figure 2). Although reference genetic databases from Sumatra, Java, and Borneo remain limited, the congruent genetic partitioning patterns within southeast Asian mammals (e.g., Leonard et al., 2015) might suggest the geographic origin of Clade C to be somewhere in Sundaic Borneo/Java.

4.2 | Genetic management in captive breeding programs

The captive breeding of wildlife in zoos and aquariums is a potential conservation strategy to alleviate the pressure on endangered wild populations and help establish and sustain insurance populations that could be reintroduced in case the wild population becomes extinct (Jewgenow et al., 2016; Maunder & Byers, 2005; Ralls & Ballou, 2013). However, in the context of pet otters, this strategy may pose other concerns, such as animal welfare, and may not alleviate the demand for otters, thus continuing to fuel the otter trade. In addition to in situ conservation efforts, controlled breeding programs outside of the range area of the Asian small-clawed otter may help prevent inbreeding and maintain the gene diversity of the species. The higher genetic diversity found in otters from zoos/aquariums compared to those from EACs/otter cafés may be due to breeding plans that minimize pairing highly related individuals. Conversely, otter cafés may have mated their subjects with closely related individuals due to the unknown origins of their otters. Zoos and aquariums, on their side, have more founder individuals contributing to greater genetic diversity in captive-bred populations.

An obstacle to the conservation of the Asian small-clawed otter is the effect of small population size in zoos and aquariums and their unplanned mating, resulting in inbreeding and random genetic drift. According to the Japan Association of Zoos and Aquariums, the Asian small-clawed otter is the most common species of otter held in captivity, and as of December 2022, 214 Asian small-clawed otters were kept in 50 zoos and aquariums in Japan. However, while Japanese zoos and aquariums conduct captive breeding management of this species based on a studbook, many captive individuals have been imported through foreign zoos/aquariums and third-party wildlife traders, with detailed geographical backgrounds unknown (Personal Communication with zoo staff). We identified multiple haplotypes in 9 of the 13 zoos/aquariums surveyed. Hap1 was found in 17 out of 43 individuals from Japanese zoos and aquariums, accounting for 40% of the total. However, Hap2 and Hap9 were found only in two male individuals, which may result in the loss of both mtDNA variations from Japanese zoo/aquarium founders. Further analysis of microsatellite loci is necessary to investigate the kinship and biparental diversity among individuals with Hap1, Hap2, and Hap9. Hence, systematic captive population management is essential to maintain a large gene pool and a realistic adaptive potential of the otters for future reintroductions to support wild populations.

To conclude, our findings suggest that most of the sampled otters in EACs and those confiscated by airport

customs in Japan originated from southern Thailand, likely through illegal trade routes. On the other hand, the origins of zoo/aquarium otters are more diverse, with more source countries besides Thailand supplying founders. There is still a limitation to the resolution for determining the provenance of otters from EACs and customs seizures, even at the level of the country. Furthermore, the efficacy of the analyses, which are based on maternally inherited mtDNA, may depend on the natural dispersal of male and female Asian small-clawed otters. For example, while some mtDNA haplotypes may be specific to a country or region, others may be widespread, thereby limiting the accuracy or precision for determining the source of an individual otter. Due to the long-distance dispersal ability of otters and the weak or lack of movement barriers toward historical gene flow, the same mtDNA haplotypes of the Eurasian otter (*Lutra lutra*) (Mucci et al., 2010) are shared among several European countries. Similarly, identical haplotypes of the Marine otter (*Lontra felina*) (Vianna et al., 2010) and the Neotropical otter (*Lontra longicaudis*) (Trinca et al., 2012) are shared across South American countries. It is, therefore, possible that some of the haplotypes that appeared to be unique to Thailand could be widely distributed in multiple countries across Indochinese or Sundaic regions. It is essential to expand the genetic reference of wild individuals across the entire distribution range of the Asian small-clawed otter *A. cinereus* and compare them with nuclear DNA as well as mtDNA to provide the accurate geographical origin of seized individuals. Understanding the origins of these captive otters in Japan and creating a regional reference database to tackle the issue of unknown origin can help identify trafficking hotspots in source countries and more effectively guide law enforcement efforts and resource allocation to combat trafficking. Moreover, nuclear DNA analysis, in addition to mtDNA, will provide accuracy for determining the geographical origin of individual otters. Additionally, it creates accountability and encourages nations to take responsibility for illegal and unsustainable legal wildlife trade within their borders.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest that could be perceived as prejudicing the impartiality of the research reported.

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SUPPORTING INFORMATION

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