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Home and hub: pet trade and traditional medicine impact reptile populations in source locations and destinations

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The pet trade and Traditional Chinese Medicine (TCM) consumption are major drivers of global biodiversity loss. Tokay geckos (*Gekko gecko*) are among the most traded reptile species worldwide. In Hong Kong, pet and TCM markets sell tokay geckos while wild populations also persist. To clarify connections between trade sources and destinations, we compared genetics and stable isotopes of wild tokays in local and non-local populations to dried individuals from TCM markets across Hong Kong. We found that TCM tokays are likely not of local origin. Most wild tokays were related to individuals in South China, indicating a probable natural origin. However, two populations contained individuals more similar to distant populations, indicating pet trade origins. Our results highlight the complexity of wildlife trade impacts within trade hubs. Such trade dynamics complicate local legal regulation when endangered species are protected, but the same species might also be non-native and possibly damaging to the environment.

1. Background

Southeast Asia is well known as a wildlife trade hotspot with diverse drivers behind the massive trade, including pet trade and medicine [1,2]. Traditional Chinese Medicine (TCM, or 中醫/中医/zhōng yī), a thousand-year-old branch of medicine, relies on a holistic and proactive approach to maintaining balance and health within one's body, by consuming a large variety of wildlife-related products, mostly plants and fungi [3]. However, its depiction in the media centres around its role in the consumption of charismatic fauna, e.g. rhinoceros, bears or tigers [4,5]. The exotic pet trade is a relatively new driver of wildlife trade [6], with growth facilitated by social media [7]. Annually, tens of millions of animals are traded in the exotic pet trade industry [8].

The impacts of both legal and illegal trade on wildlife are wide and varied, including the depletion of wild populations through poaching [1] as well as introducing alien species or populations [9–11]. In reptiles and amphibians, the pet trade is the leading cause of exotic species establishing outside of their range [11]. Invasiveness is also positively linked to commercial success in the pet trade [8]. Finally, wildlife trade is a major transmission pathway for zoonoses [12], and carriers of antibiotic resistance [13].

Depending on its scale, poaching of individuals in their native range can lead to smaller, more fragmented populations, decreasing the genetic diversity of the species at the local, regional and even global scale [14]. When the location of release is also part of the species distribution range, hybridization can occur

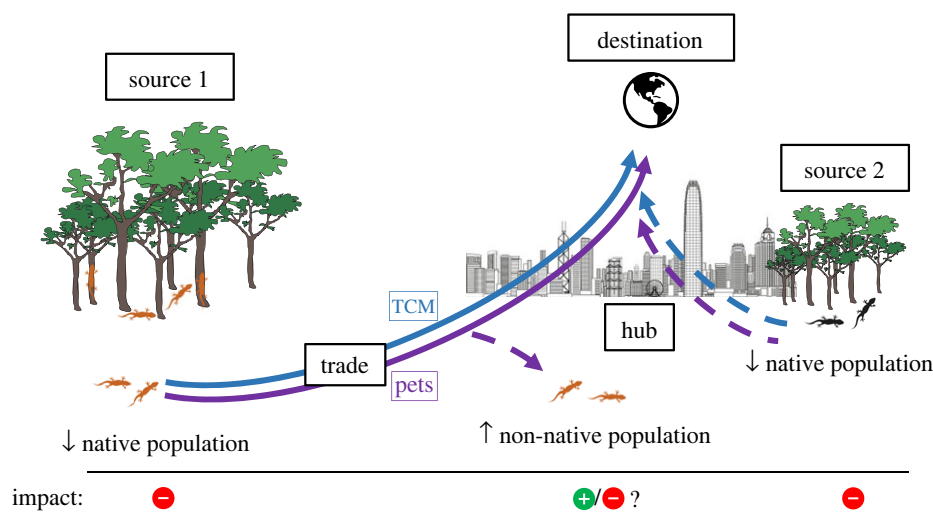


Figure 1. Representation of the consequences of TCM (blue arrows, generally traded not alive) and pet trade (purple arrows, should be traded live) for native and introduced populations at the source, hub, and destination (i.e. world). Red ‘−’ represents negative impacts, green ‘+’ represents positive impact. The blue line represents the TCM trade, the purple line for the pet trade. The solid lines represent pathways of trade from the source to destination while dashed lines represent hub-related pathways. (Online version in colour.)

between released individuals and native populations, increasing the local diversity at first, but causing a decrease in global diversity via human-mediated genetic ‘pollution’ [15]. In such cases, the release of traded pets into locations where that species also occurs can have a range of consequences, for both the source, hub and destination locations (figure 1).

Tokay geckos (*Gekko gecko*) are one of the most heavily traded reptiles in the world, both legally and illegally [16], with millions of individuals sold internationally every year, both for TCM and as pets [17,18]. Distributed throughout South and Southeast Asia, from India to New Guinea, they are composed of two morphs (black- and red-spotted) or subspecies (*G. gecko reevesii* and *G. gecko gecko*)—sometimes elevated in the literature to species level [19]. Exported from various countries across its distribution range, the species was recently (August 2019) added to CITES Annex II [20].

Owing to its unique location and set of regulations, Hong Kong, a Special Administrative Region of China, has a long history as a platform for wildlife trade in Asia [21,22] and tokay geckos are common in local TCM shops. In 2021, tokay geckos were added to the Hong Kong Protection of Endangered Species of Animals and Plants Ordinance (Amendment of Schedules 1 and 3) Order 2021, which is expected to lead to increased control measures. In addition to being a hub for import and trade of tokay geckos, Hong Kong also has several local populations. However, it is unclear whether these populations are native or introduced. First recorded sightings are from the 1950s [23], but given its geographical proximity to native populations in southern China it is possible that the species is also native to Hong Kong.

In this study, we tested whether geckos sold in TCM markets originate from local or non-local populations, using both genetic and stable isotope analysis. We then analysed phylogenetic relationships between local populations, and between local and non-local populations in order to provide insight into the impacts of trade on this species in Hong Kong. Interviews with TCM shop owners provided insights into the knowledge of current regulations and scale of the trade.

2. Material and methods

(a) Study species and system

Tokay geckos (*Gekko gecko*) are the second largest species of geckos in the world and are widespread across Asia. Although they remain listed as Least Concern on the IUCN Red List, tokay geckos are listed as Endangered in the China Red Data Book, as Threatened in Vietnam Red Data Book, and were included in the Schedule 4 of India’s Wildlife (Protection) Act of 1972 as Highly Endangered in 2014. Despite this, tokay geckos receive little actual protection throughout their natural range where populations are declining, by up to 50% in some locations [17].

Some countries like Indonesia have imposed quotas on exports for the pet trade, requiring animals to be captive-bred and exported alive. About three million tokay geckos per year were exported from Indonesia from 2015 to 2021, all dead and dried [18], with an export record of 5 974 550 in 2022 [24]. In addition to the legal breach this case raises (this quantity is well above the 25 250 quota), farming geckos on such a scale would require large/extensive breeding facilities, with over 140 000 adult females and 14 000 adult males taken care of at all times by hundreds of full-time staff, for a purchasing price of about 1 USD per animal. Considering the low purchasing price in most exporting countries of South and Southeast Asia, existence of these high-cost facilities seems more than unlikely [16,18]. Often presented as a sustainable alternative to overharvesting of wild populations, farming can also be a cover for laundering and put additional pressure on wild populations [16,25]. Interest in farming for sellers might also be very limited as it has been pointed out as a driver for decreased price, since price often follows rarity [26].

(b) Sampling design

Both *G. gecko gecko* and *G. gecko reevesii* seem to occur in different areas of Hong Kong, with two main populations described on Lantau Island and Lion Rock Country Park, and smaller populations possibly established through intentional or unintentional release from the pet trade [23]. We surveyed seven field sites across Hong Kong for which the presence of tokay geckos was known, between August and November 2020. Precise locations are kept confidential to limit risks of poaching [27]. We caught geckos by hand or butterfly net. Upon capture, we collected

morphological information on snout vent length (SVL), total length (TL), sex, morph (red- versus black-spotted) and mass. We took pictures of ventral and dorsal sides with a uniform background for further reference. We collected a small tail clipping (approx. 0.5 cm) from each animal, half stored in 70% ethanol (for genetic study) and half in an empty tube (for stable isotope analysis). As the tail is capable of regeneration this was deemed the least invasive method for this study [28]. For dried specimens, we purchased 19 pairs of dried tokay geckos (electronic supplementary material, figure S1) allegedly originating from China, Thailand and Vietnam from 18 shops in Hong Kong (electronic supplementary material, table S1). All shops were given an identification letter to preserve anonymity. We also obtained shed skins from two pet tokays that had been in captivity more than 1.5 years, from volunteer pet owners. The two pet owners mentioned that the tokay geckos they purchased from local pet shops were sold as 'wild'. Additionally, we received the corpse of one wild individual, found dead in Lantau Island.

(c) DNA extraction, sequencing and phylogenetics

We extracted DNA from tail tissue (wild-caught tokays) and dried ventral tissue (dried tokays) using DNeasy Blood & Tissue extraction kits (QIAGEN, Hilden, Germany) following the manufacturer's recommendations. We amplified the complete NADH dehydrogenase subunit 2 (ND2) gene (1038 bp) using conventional PCR and a set of primers designed by Wang *et al.* [29] – F: 5'-GGT-TAA-AYY-CCC-CTY-ATT-TCC TA- 3', R: 5'-GYG-TCT-GRR-TTG-CAR-TCA-GAR-GA-3'. PCR was performed in a reaction volume of 20 μ l, containing 1 \times Biotechrabbit™ Lyo Hot Start PCR Master Mix, 1 mM of primers, 1 μ l of Bovine Serum Albumin, and 2 μ l of genomic DNA as template. We performed amplifications with the following programme: 2 min at 95°C, 35 cycles of 30 s at 95°C, 30 s at 57°C, and 1 min at 72°C with a final extension step of 7 min at 72°C. We visualized by electrophoresis on a 2% agarose gel. We purified PCR products using QIAquick PCR purification kit (QIAGEN, Hilden, Germany) following manufacturers' recommendations and sequenced them using an ABI 3730xl DNA Analyzer at the Centre for PanorOmic Sciences (CPOS), Li Ka Shing Faculty of Medicine HKU.

We assembled and edited genetic sequences using GENEIOUS PRIME version 2021.2.2 (Biomatters Ltd., Auckland, New Zealand). Partial gene sequences (NADH dehydrogenase subunit 2; ND2) of *G. gecko*, collected in the field or from TCM shops, were aligned with previously published sequences using MUSCLE v 3.8.425 [30]. To be included, GenBank sequences had to fit three criteria: they (1) had to be supported by a peer-reviewed article, (2) were long enough (greater than or equal to 752 bp) for comparison, and (3) represented all clades described to this day for this species. We trimmed all sequences to 752 bp to fit sequences retrieved from GenBank. We checked manually the multiple alignment for accuracy. A phylogenetic tree was estimated using the maximum-likelihood method and GTRGAMMA substitution model implemented in RAxML v 8.2.12 [31]. One hundred multiple inferences were performed, and the best tree was selected for comparison with the 1000 bootstrap replicates. We visualized the tree in INTERACTIVE TREE OF LIFE v.5. (iTOL, [32]).

(d) Stable isotope analysis

We used stable isotope analyses (SIA) to infer breeding conditions and/or geographical origin of TCM geckos [28,33]. We compared $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from tail samples from wild-caught and TCM geckos. We selected tail tissue as it has a lower turnover in isotopic ratios compared to other tissues in lizards and therefore represents better the long-term diet [34]. SIA has previously been used on a wide range of animals, including reptiles, to differentiate diet between different breeding conditions (captive, semi-captive, or wild) based on differences in the ratios of heavy to light isotopes

of C and N in their diet ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$; [28,33]). Here, we studied the potential overlap between the diet of TCM shops and HK wild-caught tokay geckos.

For SIA, 0.5 cm of the tip of the tail of the wild and TCM shop individuals was dried at 60°C in a chamber for 24 h minimum and subsequently cut into small aliquots of approximately 1 mg (1.35 ± 0.12 mg) and loaded into tin capsules. Analysis was conducted using an EA-IRMS (Eurovector 3028-Nu Instruments Perspective IRMS) at the Stable Isotope Ratio Mass Spectrometry (SIRMS) Laboratory at HKU, using a certified standard (Indiana University acetanilide, ($\delta^{13}\text{C} = -29.53$ ‰, $\delta^{15}\text{N} = +1.18$ ‰) to correct the resulting sample values. Results were reported as a ratio to the reference values from Hong Kong and expressed in δ units in the conventional permil notation, where $\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ (adapted from van Schingen *et al.* [28]).

We performed Welsh *t*-tests to test for differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between tokay geckos sampled from the wild and those purchased from a shop in R v. 4.0.3 [35]. We constructed a biplot of $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ in wild and shop samples using the package *ggplot2* [36] and drew ellipses representing 95% confidence intervals using the *stat_ellipse* function included in *ggplot2*. We then investigated whether different haplogroups had different isotopic signatures: first, using a Kruskal–Wallis test and second, using two Steel–Dwass All Pairs multiple comparison tests, with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as response variables, and haplogroups as explanatory variables [37].

(e) Shop surveys

We visited 18 registered TCM shops on three different days between February and April 2021 in three main districts of Hong Kong (Sham Shui Po, Sheung Wan, and Yau Ma Tei) and carried out nine interviews in Cantonese. Questionnaires were composed of a series of open- and closed-ended questions (electronic supplementary material, table S2; adapted from [38]), around several main themes: background on the shop, consumption of geckos, origin of the products and import, and trends. Interviews were conducted by the same interviewers in Cantonese following a semi-structural oral format. Answers from interviewees were written down and later translated into English for further analysis. Each interviewee gave consent and was offered the option to skip any question he or she was not comfortable answering. Surveys were later anonymized.

3. Results

We collected 53 individuals from seven different locations across Hong Kong (electronic supplementary material, appendices S1 and S4). Black-spotted morphs were found in all seven locations, while the red-spotted morph was only found in one site (table 1). Some individuals were noted as 'undetermined' when the morph was unclear (electronic supplementary material, figure S2).

(a) Phylogenetic analysis

We obtained 81 new sequences of the ND2 mitochondrial gene; 51 from wild-caught *G. gecko*, 29 from dried specimens from TCM markets, and one from a captive individual. All sequences were deposited in GenBank (Accession numbers: ON098980–ON099060). We found 251 segregating sites, of which 205 were parsimony informative sites and 46 were singleton sites.

Five *G. gecko* clades have been previously described, namely clades A divided into two subclades A1 and A2, B, C, D and E, which contain 10 haplogroups (G1–G10)

Table 1. Morphological characteristics of wild-caught individuals from seven wild populations across Hong Kong.

location	population	species/morphs present	mean SVL \pm s.d. (mm)	mean total length (mm)*	mean body mass (g)*	n (number of adults)	sex of adults
Hong Kong Island	BR	Black-spotted	136.35 \pm 42.88	253.57 \pm 77.45	41 \pm 31.68	5 (4)	2M:2F
	AC	Black-spotted	117.58 \pm 36.16	208.87 \pm 52.5	65.8 \pm 35.27	10 (6)	3M:1F (+2NA)
Lantau Island	TF	Black-spotted	123.32	222.42	49	1 (1)	NA
	WH	Black-spotted	134.52 \pm 29.22	234.75 \pm 56.08	70.2 \pm 30.51	10 (9)	7M:2F
New Territories	MS	Red- + Black-spotted + Undetermined	130.6 \pm 49.75	242.88 \pm 91.64	72 \pm 36.12	6 (5)	3M:2F
	PL	Black-spotted + Undetermined	113.71 \pm 44.71	207.64 \pm 79.35	48.8 \pm 42.32	10 (6)	5M:1F
	LR	Black-spotted	131.35 \pm 31.24	233.18 \pm 54.76	64.3 \pm 33.39	10 (8)	3M:1F

[29,39,40]. Most *G. gecko* captured in Hong Kong, as well as one specimen from TCM shops (i.e. FCHGX2) clustered within subclade A1, haplogroup G7 with sequences from Guangxi, China. Within this subclade, the New Territories (PL and most of LR) and Lantau Island (WH and TF) populations clustered in the same subgroup (bootstrap value = 83), suggesting some genetic structuring among the Hong Kong populations. The last six individuals (MS and two AC) clustered within two subclades of clade B. Five specimens, collected in MOS, fell within the haplogroup G6 subclade containing specimens from peninsular Thailand as well as a non-native specimen from southern Florida, USA. These results were consistent with visual identifications; while most Hong Kong tokays were black-spotted, the MS population was principally composed of blue-skinned, red-spotted individuals. The remaining two specimens captured in AC (i.e. AC2 and AC4) as well as one specimen obtained in a TCM shop (i.e. FCHGX1) placed within haplogroup G2 containing specimens from Northern Thailand (figure 2).

The majority of *G. gecko* obtained from TCM shops clustered within clade B, haplogroup G1, which includes specimens from northeast Thailand, Central and Northern Laos, and Guangxi (China). The last four specimens from TCM shops fell within the remaining clades. Specimens TCHNC1 and TCHNC2 clustered within subclade A2, haplogroup G3 which contains specimens from Cambodia, northeast Thailand, West Malaysia, Guangxi (China), Indonesia, East Timor and Vietnam. Specimen KCH2 placed within clade D, haplogroup G4 that includes specimens from northeast Thailand and Central Laos, and specimen RTH1 placed within clade E, haplogroup G5, which contains specimens from Northern Thailand (figure 2). Individuals belonging to the same pair were on three occasions clustering into different clades (KCH1/KCH2, RTH1/RTH2, FCHGX1/FCHGX2). Finally, the captive *G. gecko* specimen (CAPT3) clustered with a specimen from Vietnam within subclade A2, haplogroup G3 (figure 2).

(b) Stable isotope analysis and shop surveys

First, carbon and nitrogen ratios were significantly higher in tokay geckos from shops than from HK wild populations ($t = -7.27$ and $t = -13.61$, respectively, and $p < 0.0001$ for both; figure 3), indicating different food sources for TCM and HK wild-caught individuals. There was little overlap between the two groups (overlap of $\delta^{15}\text{N}$ of shop and wild = 11.9%; of $\delta^{13}\text{C}$ of shop and wild = 19.8%), with only four TCM individuals overlapping with the 95% confidence interval of HK wild Tokays: FCHGX1, QTH2, KCH1 and KCH2. Despite being of comparable sample size, the TCM shops ellipse was larger than the HK wild ellipse, suggesting multiple food sources and locations for the TCM individuals (figure 3). We found some significant differences in isotopic ratios between haplogroups (Kruskal-Wallis; for $\delta^{15}\text{N}$: $H = 47.3$, d.f. = 6, $p < 0.0010$; for $\delta^{13}\text{C}$: $H = 46.1$, d.f. = 6, $p < 0.001$) (electronic supplementary material, figure S3), specifically between differences $\delta^{15}\text{N}$ of G1 and G6 (Steel-Dwass multiple comparison test; $p = 0.028$) and G1 and G7 (Steel-Dwass multiple comparison test all multiple comparisons; $p < 0.0001$). For $\delta^{13}\text{C}$ we only noted a significant difference between G1 and G7 (Steel-Dwass multiple comparison test all multiple comparisons; $p < 0.0001$), but not between any other pairs (electronic supplementary material, figure S4).

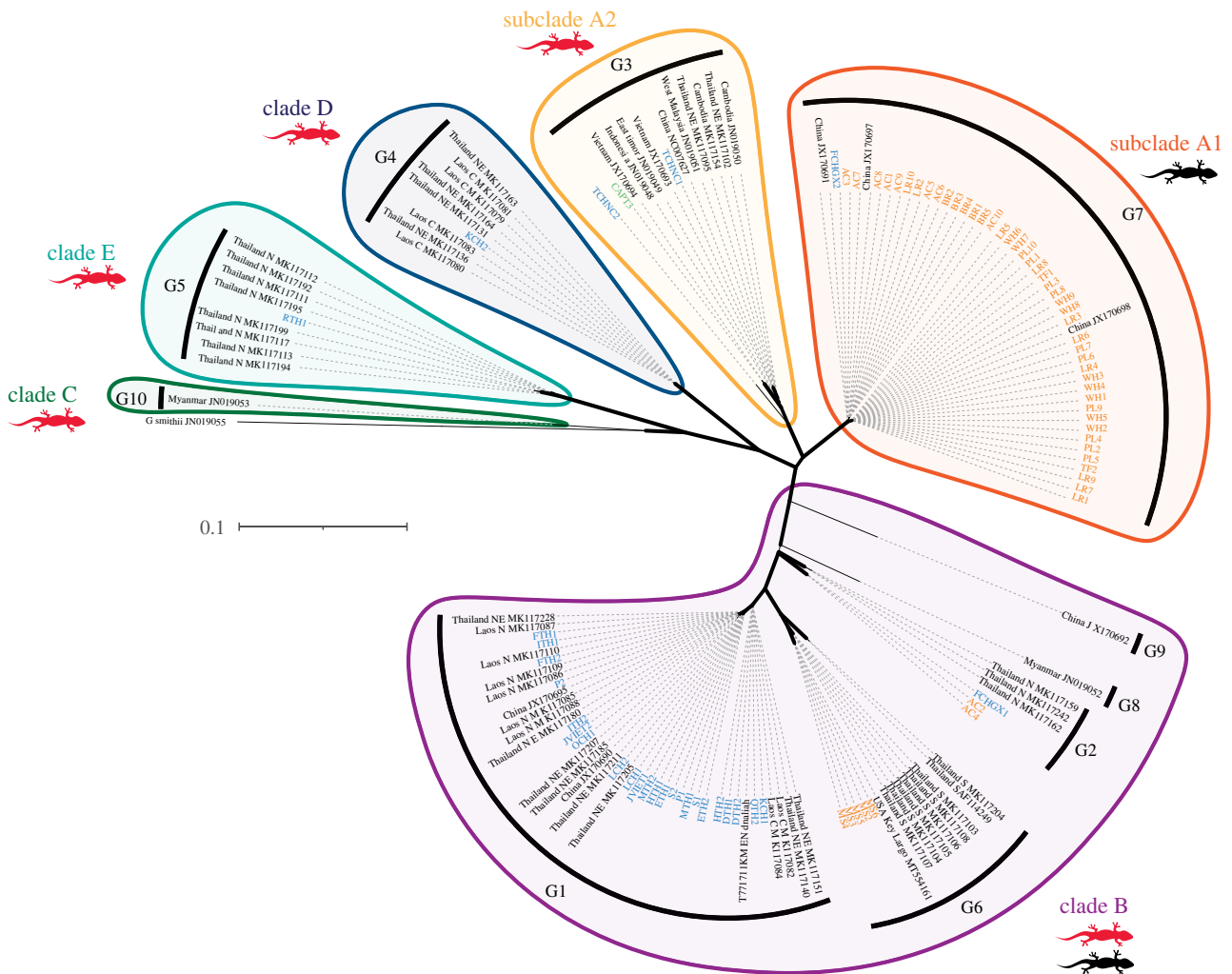


Figure 2. Phylogenetic tree of *G. gecko* based on partial ND2 gene (752 bp) using maximum-likelihood method. Sequences from Hong Kong wild-caught individuals ($n = 51$) are written in orange, from TCM shops ($n = 29$) in blue, and from a captive individual ($n = 1$) in green. Clade (a–e), subclade (A1 and A2) and haplogroup (G1–G10) classification follow Saijuntha *et al.* [29] and Fieldsend *et al.* [40]. *G. smithii* was used as an outgroup. The scale-bar indicates the expected number of substitutions per site. Bootstrap values > 70 are represented by thick lines. Visualized with iTOL v.5 [30]. Red and black silhouettes represent red- and black-spotted geckos morphs either observed or described in relevant papers. (Online version in colour.)

Out of the 18 TCM shops surveyed, nine representatives (50%) agreed to undergo interviews (electronic supplementary material, figure S5). All interviewees asserted that tokay geckos were imported from elsewhere as dried products. Five shops declared importing from Thailand (56%), one from Vietnam (11%) and six from China (56%), and only one shop declared having two different origins (China and Thailand) sold at the same time (electronic supplementary material, figure S6). Eight (88%) shopkeepers believed tokay geckos to be farmed, but one (11%) of them also mentioned selling wild individuals from Thailand. One shopkeeper stated that they did not know the geographical origin. Imports from Indonesia were mentioned spontaneously as a custom from the past by two shop representatives (22%), but they stated that it was no longer the case. While the trade in whole tokay geckos appears to be less popular than it used to be ($n = 4$) or similarly popular ($n = 3$), new means of consumption, such as powder to mix in liquids, may be emerging ($n = 2$).

We observed very little knowledge on the existing regulation for this species: a clear minority ($n = 2$) believed that the Tokay gecko trade was regulated by permits, of which one trusted it was the sole responsibility of the supplier, while the other mentioned the responsibility to be shared by the importer.

The remaining shop representatives ($n = 7$), including the shop owners, declared not knowing of any regulation or permit.

4. Discussion

For tokay geckos, wildlife trade impacts source populations throughout the species' range through the removal of individuals for the TCM and live exotic pet trade. Our genetic analysis shows that TCM trade in Hong Kong is not likely supplied by local wild populations, but by imports from Southeast Asia. Additional information from SIA supports our genetic findings, as we detected very little overlap in isotopic signatures between TCM and Hong Kong wild tokays. Trade also leads to mixing of populations through introductions related to the live pet trade. We found that at least two Hong Kong wild tokay populations were likely established from released pets. TCM shopkeepers had inconsistent knowledge of legal regulations in the trade of tokays, which suggests that current regulations are not sufficient to stem the trade in this species. Together our results highlight how multiple drivers of wildlife trade (in this case, pet trade and TCM) can have consequences for populations throughout a species' range (figure 1).

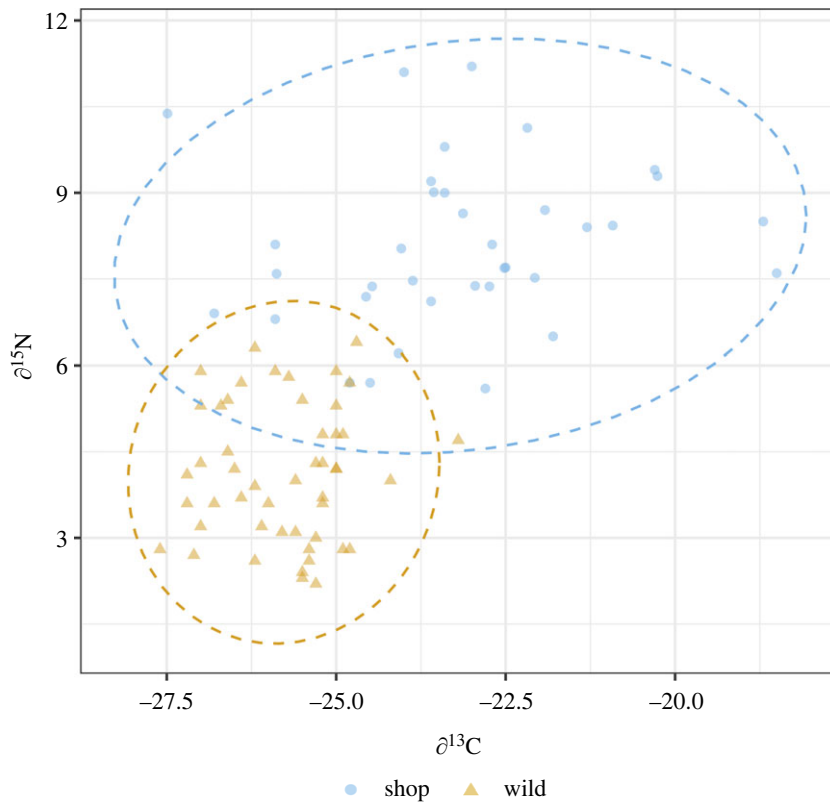


Figure 3. Biplot of $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ of wild HK populations (orange triangles, $n = 49$) and TCM individuals from shops (blue dots, $n = 36$). Dashed line represents 95% CI of each group. (Online version in colour.)

(a) Impacts on source populations

We found individuals being sold for TCM from at least five unique populations, revealing a geographically broad sourcing of tokay geckos for the trade. We successfully identified relationships with individuals from Thailand (North and Northeast at the minimum), Laos (Central and North), Mainland China (Guangxi province) and probably other Southeast Asian countries (e.g. subclade A2, with reference sequences from Indonesia, Vietnam, Cambodia, West Malaysia and China). In some cases, the advertised origin of an individual did not match the origin identified through genetic analysis. Moreover, while tokay geckos were always sold as a pair for TCM (electronic supplementary material, figure S1) (supposedly one male and one female, for yin-yang purposes, see [17]), individuals within the pair did not always originate from the same location (sometimes being from different countries), despite what the label and/or supplier stated. This indicates that: (i) labels cannot always be trusted as only one origin out of two is advertised, and (ii) pairs are likely assembled between the exporting source and sellers in Hong Kong, probably at the retailer level. While genetic analysis is a powerful tool to identify geographical provenance, pinpointing an exact location an individual came from depends on the availability and variability of sequences from across the species' range [40–42]. With millions of tokay geckos exported by Indonesia each year [18] and very few sequences available on GenBank, it is urgent to improve the spatial resolution of genetic data for the species.

Economics and ease of collection, as well as supply and demand, dictate the balance between local collection of species and importation from overseas. Despite high levels of trade in tokay geckos, our results reveal that local Hong

Kong tokays are not likely used to supply local TCM trade, at least not presently. Similarly, snake meat used in snake soup in Hong Kong was principally imported from Mainland China years ago and later relied on imports from Indonesia, rather than sourcing it locally [38]. The relative low abundance of tokay geckos in Hong Kong probably prevents hunting activity as the returns would be minimal compared to elsewhere in Southeast Asia. As the primary source of tokay geckos for trade in Hong Kong is Southeast Asia, legal cooperation between China and Southeast Asia is thus essential in combatting the large trade flow in tokay geckos and other species [5]. Furthermore, while the CITES listing of species can be an important first step in trade regulation, intensive monitoring of both demand and supply across species distributions must supplement tracking of trade [43].

For some species, sustainable trade might be possible if individuals can be successfully bred in captivity. In order to monitor such efforts, it is essential to be able to determine whether an individual was captive-bred or wild-caught. According to most shop keepers selling dried tokay geckos that we interviewed (88%), TCM tokays were bred in captivity. However, we also identified packages advertising wild origin, at relatively higher prices. Our stable isotope analysis demonstrated that TCM tokays were not feeding on the same food sources as local wild tokays from Hong Kong, providing evidence that the TCM tokays were not of local origin. We also found some differences in isotope ratios between haplotypes, particularly between clade G1 and clades G6/7. Tokays in the TCM trade had a much wider dietary range than those caught locally in Hong Kong, suggesting that tokays in the trade came from several origins and not from a single breeding farm or poaching site. However, the broad range of values measured in TCM tokays could also

result from temporal variation (e.g. seasonal differences) in diets. Further research is needed to confirm whether these tokays for sale were captive-bred or wild, for example by comparing with samples from captive-bred animals [31,36]. Farming can benefit conservation if it follows clear rules [44], including sold animals benefiting from equal status of farmed versus wild-caught products, which is not what we observed here. Moreover, wildlife farming should be more cost-efficient than poaching and not dependent on poaching for maintaining activities [44]. These conditions were not met in other studies looking at the trade in tokay geckos [16], or green pythons for example [45]. For farming to be part of a sustainable trade practice, the process must be transparent and access to wildlife farms made easier for independent organizations.

(b) Impacts of pet trade

Live animal pet trade poses threats not only for the source populations, but also potentially for release populations [10]. Pets that are released either intentionally or unintentionally can impact local populations of the same species through the spread of non-local genetic variation or diseases. Introduction of genetically divergent individuals into a new territory can have a wide range of consequences on the native population, from almost none (e.g. when introduced animals fail to adjust and die shortly after), to increase of the overall local genetic pool when there is no interaction with local populations of the same species, to the loss of genetic diversity through the loss of local adaptations or through hybridization. This loss of diversity, also known as ‘genetic pollution’, has been described in other Hong Kong herpetile taxa (turtles [15] and frogs [46]). Mercy release is a common Buddhist and Taoist practice which involves the liberation of captive animals for spiritual purposes and constitutes a primary source of introductions in the region [46,47]. Moreover, some pet owners may choose to release their animals on ‘compassion’ grounds (i.e. a belief that the animals will have more ‘freedom’ and habitat quality in the wild compared to captivity) or because they no longer wish to care for their pet for different reasons (e.g. some turtles or iguanas when they become too big, e.g. red-eared sliders in Yeung [48]). Tokay geckos used to be sold for approximately 1 USD in snake shop soups in Hong Kong and were released into houses as pest control. While we cannot be sure of the events that led to the introduction of red-spotted geckos in Hong Kong, we have shown that at least two local populations are of Southeast Asian origin. There is little genetic differentiation between tokays from Hong Kong and from Southern China, so while Hong Kong populations are for the most part closely related to each other, it cannot be ruled out that they are all surviving descendants of successful past introductions from Southern China in the 1950s [23].

Analysis of mtDNA is not sufficient to measure current gene flow between local and introduced individuals, but future studies incorporating whole genome sequencing techniques could provide more information on the impacts of these introduced individuals on local populations. As Leven and Corlett [49] describe for birds, much of Hong Kong’s biodiversity is the result of a long and complex history of animal local extinction and recolonization (both natural and human-mediated). Given this, we do not recommend culling or removal of these populations. However, the prevention of further releases of captive animals in the wild should be a

priority and releases made illegal (supplemented by education and further monitoring) given the significant negative consequences possible for native species [46].

(c) Recommended management actions for trafficked species in trade hubs

Events of poaching from Hong Kong (likely for the pet trade) have been shared on social media in recent years. The addition of tokay geckos to the Hong Kong Protection of Endangered Species of Animals and Plants Ordinance (Amendment of Schedules 1 and 3) Order 2021 will help law enforcement prosecute offenders and hopefully dissuade further poaching. However, trading a protected species in TCM and pet shops without clear regulation results in mixed messaging to the public and could facilitate overexploitation [50]. Furthermore, farming of tokays is so poorly regulated that it is generally regarded as a scam for laundering wild animals [16] and therefore cannot at present sustainably feed the trade. Laundering of one species can sustain or replace trade in other species [51] while legalization of trade of one new reptile species in one part of the world results in the illegal smuggling of reptiles in other locations [52]. Effective management of the illegal wildlife trade is a multifaceted global issue that requires local and international coordination and consistency.

The post-2020 Convention on Biological Diversity report includes an objective of ‘safeguarding at least 90% of genetic diversity of wild and domesticated species’ by 2050 (<http://www.cbd.int/>). In the case of tokay geckos, we argue that heavy international trade and rapid erosion of their habitat are sufficient arguments to increase their conservation status throughout its range [20]. Because of the high level of genetic structuring between populations and generally small population sizes, conserving the tokay gecko effectively requires protection at the population level throughout its range [39]. As a first step, including a genetic component in the IUCN Red List criteria could help bridge the gap between science and conservation practice [53], providing evidence for focusing conservation effort on genetically unique populations. Second, because of the extra economic cost of monitoring the trade, financial or technical incentives should be provided to encourage developing countries to pursue sustainable trade practices, equivalent to those offered by the Paris Agreement in emissions reduction [54].

Ethics. We obtained ethical clearance from the Human Research Ethics (ref. EA210006) for our interviews and from the Department of Health for manipulating wildlife (ref. 20-711 and 20-712). Permits to conduct our field study were granted by the Committee on the Use of Live Animals in Teaching and Research (ref. 5430-20) and the Agriculture, Fisheries and Conservation Department ((115) AF GRCON 11/17 Pt.6).

Data accessibility. DNA sequences are available on Genbank (accessions ON098980–ON099060). Capture records, stable isotope, and shop data are available from the Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.r4xgxd2gc> [55].

The data are provided in electronic supplementary material [56].

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funding acquisition, methodology, supervision, writing—review and editing; T.C.B.: conceptualization, funding acquisition, project administration, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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