



Trade in Prevost's squirrels: legality, risk for introduction and disease transmission

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Abstract

Squirrels traded for pets or consumption have the potential to be vectors for zoonotic disease transmission and to establish themselves as invasive species. *Callosciurus* spp. (Greek for beautiful squirrel) are popular in the pet trade due to their medium size and many colour variants, though several feral populations have established themselves in various parts of the world and these wild-caught individuals can carry and spread infectious diseases. Here, we investigate the live trade in Prevost's squirrels (*C. prevosti*) in Indonesia where they are naturally found on the islands of Sumatra, Bangka and Borneo. Between 2016 and 2024, we recorded 284 Prevost's squirrels for sale, viz., 115 in the physical markets and 169 online. We detected the species for sale in Sumatra (13 individuals), Bangka (7) and Borneo (3), i.e. within their natural range, but also on Java (242) and Bali (4). The mean asking price per individual was US\$63, and younger individuals commanded higher prices than older ones. Asking prices were not higher in cities further away from the species' native range nor in cities with higher purchasing power. All individuals were wild-caught, and with a domestic quota of five individuals allowed to be traded as pets per year (45 over the study period) most of this trade is illegal under Indonesian law. This is distinctly different from trade in Prevost's squirrels in for instance Europe or the USA where legally captive-bred individuals are offered for sale. In Indonesia the illegal trade happens in the open and despite the risk of the spread of zoonotic diseases wherever it is traded there appears to be little incentive on the side of the authorities to curb this trade. Their widespread availability on Java and Bali risks the accidental or deliberate introduction on these two islands. Better coordination is needed between the Indonesian authorities, online sales sites, pet traders and consumers to stop the sale of illegally obtained Prevost's squirrels to limit the risk of them becoming invasive species or contributing to the spread of emerging infectious diseases.

Keywords Convention on biodiversity · Conservation · Indonesia · Invasive species · Wildlife trade · Zoonosis

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Introduction

The trade in squirrels, either for pets, for consumption or for traditional medicine, is of global concern, as they are known to be particularly effective vectors of disease transmission to other mammals including humans (Masuzawa et al. 2006; Greatorex et al. 2016; Schlottau et al. 2017; Cadar et al. 2021; Banda et al. 2022; Nawtaisong et al. 2022). The trade in live animals has also introduced squirrels into regions where they did not occur previously, and several species of squirrel have established feral populations which are considered invasive (Oshida et al. 2007; Sandro 2008; Bertolino 2009; Martinoli et al. 2010; Tran et al. 2022; Bertolino and Lurz 2013; Guichón et al. 2023; Tamura and Yasuda 2023).

In 2021, Mazzamuto et al. (2021) reported on the trade in Pallas's squirrel (*Callosciurus erythraeus*) and Finlayson's squirrel (*C. finlaysonii*) in areas outside of their native range (i.e. mainland Southeast Asia) and how this linked to the establishment of feral populations in countries such as Japan, Hong Kong, France, Italy and Argentina. Both species are strikingly coloured, with many colour variants, which clearly makes them appealing as exotic, novelty, pets (*Callosciurus* is Ancient Greek for beautiful squirrel). Directly south of the distribution range for Pallas's and Finlayson's squirrel, Prevost's squirrel (*C. prevosti*) is found, a species that is similarly strikingly coloured, again with many colour variants (Lurz et al. 2017). Unlike its two congeners, there have been no reports of their trade outside their native countries. If not at present, certainly in the past the species must have been traded internationally in reasonable numbers, as the Zoo Information

Management System lists 73 zoological collections that hold Prevost's squirrel and there are an additional 25 non-accredited zoos that also keep the species (www.zootiereliste.de).

Prevost's squirrel's natural distribution range is in the Thai-Malay Peninsula, roughly south of the Isthmus of Kra, and on the islands of Sumatra, Borneo, and smaller islands within this region (Duckworth and Hedges 2008) (Fig. 1). The species does not occur, or no longer occurs, in Singapore, and the inclusion of Bunguran, part of the north Natuna Islands, by Cassola (2016) is probably in error as the species occurs only on Serahan which is part of the south Natuna Islands. Prevost's squirrel is also found in northernmost Sulawesi, most likely introduced by humans. There is some ambiguity whether the species naturally occurs on the island of Bangka. Cassola (2016) does not list the species as present, but Lurz et al. (2017) do. This latter record can be traced back to Schlegel (1863). The species is not naturally present on Belitung, adjacent to Bangka, but for at least the last 120 years a feral population has been present on the island of Mendanau, off the coast of Belitung (Vorderman 1901).

In terms of domestic trade, there is limited information. Vorderman (1901) noted that over a century ago, Prevost's squirrels were exported from Sumatra to Java and that they were much loved as pets by the Europeans and Chinese living there. Duckworth and Hedges (2008) and Cassola (2016) state that in parts of Sarawak (Malaysian Borneo) it is very heavily hunted for the pet trade, referring to a personal communication with B. Gimán and K.H. Han but without providing any details.

Fig. 1 Distribution range of Prevost's squirrel (*Callosciurus prevosti*) in Thailand, Malaysia, Brunei and Indonesia (yellow) (after Cassola 2016 and Lurz et al. 2017) with names of geographic locations (italics and bold) and cities (plain text) mentioned in the text



In Indonesia, and to a lesser extent Malaysia and Singapore, keeping wild-caught animals as pets is (or until recently was) very common. In most larger cities, there are animal markets that on a daily basis openly offer 100s to 1000s of wild-caught birds and mammals, native to the country, for sale (Nash 1993; Nijman et al. 2018; Maulany et al. 2021). Less common species (i.e. ones that are rarely offered for sale) or rare species (i.e. ones that may be more difficult to source) are often sold at a premium (Marshall et al. 2020), but a wide range of species are sold. Indonesia has a comprehensive regulatory system in place for the trade in non-domesticated species (Soehartono and Mardiasuti 2002; Leupen et al. 2020). Species that are legally protected cannot be caught or sold, non-protected species can be harvested and sold commercially provided a harvest quota has been set for them, and non-protected species that do not have a harvest quota cannot be harvested or traded. In the markets, however, it is common to see protected species or species that do not have a harvest quota offered for sale (Noerjito and Maryanto 2001; Nijman et al. 2018); enforcement is lax and only very rarely are animals seized in the markets. The one seizure we are aware of is by Pei Pei (2019) who reported on a seizure of more than 400 protected animals from pet shops in Sebu in Malaysian Borneo and that included one or more Prevost's squirrels.

Shepherd et al. (2004) reported on the trade in Prevost's squirrel in Medan, North Sumatra, which is within the species' natural range. They observed a total of 224 individuals offered for sale in three animal markets between the years 1997 and 2003. On average, between one and six Prevost's squirrels were recorded per survey. They were recognised as novelty pets, i.e. unusual and attractive species that, compared to other squirrels, were relatively rare in trade (Shepherd et al. 2004). Other than Shepherd et al. (2004) and Pei Pei (2019), we were not able to find any other records of Prevost's squirrels recorded within the wildlife trade.

Prevost's and other *Callosciurus* squirrels have been linked to zoonotic diseases, mostly in countries outside their natural distribution range, and in the EU, direct contact with exotic squirrels is discouraged (Tappe et al. 2018). In Japan, Pallas squirrels were found to host a range of mites, fleas and ticks, with the potential to affect other native species (Katahira et al. 2022). A single introduction of the variegated squirrel bornavirus 1 from a Prevost's squirrel led to fatal encephalitis in breeders and zoo caretakers in the Netherlands and Germany (Tappe et al. 2019). In Italy, an introduced population of Finlayson's squirrel suffered from cryptococcosis (Iatta et al. 2015) and two herpesviruses and one of polyomavirus were detected in an introduced population of Pallas squirrels (Schulze et al. 2020). No research has been conducted on the presence (or absence) of zoonotic diseases in Prevost's squirrels in Indonesia, Malaysia, Brunei or southern Thailand.

We report on the trade in the Prevost's squirrel in physical markets on Java and Bali and from online platforms throughout Indonesia, and link this to the risks of accidental introduction and the spread of emerging zoonotic diseases. Based on studies conducted on the online trade in other exotic pets in Indonesia and other parts of Southeast Asia (Iqbal 2015; Morgan and Chng 2018; Siritwat and Nijman 2018; Fink et al. 2021), information provided on online discussion groups, and comparison with data from physical animal markets in Indonesia (Nijman et al. 2019), we tested six (ecological and economic) relationships described in Table 1.

Materials and methods

Data collection

Between August 2016 and February 2020 and from March 2021 to January 2024, we regularly conducted surveys on a number of bird and animal markets in Java and Bali (i.e. outside the natural range of Prevost's squirrels) that frequently offer mammals for sale (the break was introduced due to travel restrictions imposed by Covid-19). The survey team comprised of authors V.N., A.A., J.C., T.D., I.N.A.D.P., C.S.R. and K.A.I.N, with typically one or two members of the team conducting individual surveys. We walked through markets slowly, recording numbers and species either on mobile phones or memorising numbers and recording them in a notebook directly after leaving the market. Back alleys were not surveyed. There was no need to use undercover techniques as the trade happens openly. We noted species and prices when possible, and photographs were taken opportunistically. We requested asking prices from the vendors without bargaining, and we did not purchase any birds or other wildlife. Animal markets are open to the public and are open all days of the week, from early morning to early evening (in addition, there are animal markets that are only open on certain days of the Javanese calendar, such as Pon or Wage, but these animal markets are often smaller and were not included here). Traders offer a wide range of bird and mammal species for sale, including native species that are legally protected, native species that can be traded in limited numbers and non-native species that are imported into the country. Almost all species are offered alive and are sold alive as pets (the exceptions being bats and plantain squirrels (*C. notatus*) that may be slaughtered in the market and are sold for medicinal purposes: Morcatty et al. 2022). In the larger animal markets (e.g. Pramuka, PASTY, Bratang), mammals may be displayed in the back or in specific sections, but in the smaller animal markets, they are displayed throughout the market. A survey could last from around 2

Table 1 Predictions concerning specifics on the trade in Prevost's squirrels (*Callosciurus prevosti*) in Indonesia

Prediction	Rationale	Variables tested	Studies in support of prediction
Squirrels under 3 months of age are more expensive than older ones	For proper bonding with humans, squirrels must be young; older individuals remain wild	Asking price and ages provided by vendors	In wild mammals, younger animals are often more expensive as they still can be tamed or are considered cuter: Kabasawa (2009); Siritwat and Nijman (2018)
Asking prices are dependent on the purchasing power of consumers	In poorer regions consumers have less disposable income to spend on exotic pets	Mean asking price in a city and government recommended minimum monthly wage for 2023	In Javan ferret badgers (<i>Melogale orientalis</i>) there is a positive relationship between a city's minimum wage and asking price: Thomas et al. (2021).
Asking prices are dependent on distance to sourcing area	Transport costs add to the overall cost of bringing squirrels to market, and given that most of the trade is illegal, longer travel time increases the likelihood of detection	Mean asking price in a city and distance to either Sumatra or Borneo	Prices of the same wildlife product, e.g. ivory bangles, increase from the central trading points: Nijman and Shepherd (2014)
In cities with few squirrels for sale prices are higher	Rarity has a premium and where fewer squirrels are on offer prices go up	Mean asking price in a city and number of squirrels offered for sale in city	Humans place exaggerated value on rarity, rarer species are thus more desirable, and more expensive: Courchamp et al. (2006); Holden and McDonald-Madden (2017)
More individuals are offered for sale within than outside their native range	Within native range there are more opportunities to source animals	Total number of individuals and number of cities where the species was offered for sale within and outside native range	In primates, species are offered for sale primarily on the islands on which they occur naturally: Nijman et al. (2021).
Number of individuals offered for sale is dependent on distance to sourcing area	Transport costs add to the overall cost of bringing squirrels to market	Total number and distance from marketplace to either Sumatra or Borneo	See references above

h for some of the smallest animal markets (e.g. Cikurubuk) to a full day for the largest (e.g. Pramuka). In September 2022 and March 2024 we searched for published reports of market surveys that reported on Prevost's squirrels for sale, both in Indonesia and other countries.

We focus here on those markets that were visited at least seven times over this period (i.e. on average twice a year). These included three wildlife markets in Jakarta: Pramuka (16 surveys; 2016–2022), Barito (28 surveys; 2016–2022), Jatinegara (30 surveys; 2016–2024); three in West Java: Sukahaji, Bandung (45 surveys; 2016–2024), Kerkhof, Garut (36 surveys; 2016–2023), Plered, Cirebon (8 surveys; 2016–2020); two in Central Java: Karimata, Semarang (10 surveys; 2017–2019) and Depok, Surakarta (7 surveys; 2017–2019); one in Yogyakarta: PASTY (8 surveys; 2017–2020); one in East Java: Bratang, Surabaya (7 surveys; 2017–2020); and one in Bali: Satria, Denpasar (11 surveys; 2017–2024). In addition, we compiled data from other wildlife markets that were visited fewer times over this period to assess if Prevost's squirrel was recorded. From west to east, these were as follows: Kebayoran Lama in Jakarta, Tj Empang in Bogor, Cikurubuk in Tasikmalaya, Kupang and Turi in Surabaya, Sangla in Denpasar and Sindu in Mataram (Morcatty et al. 2022).

In September 2022, August 2023 and March 2024, we searched Indonesia's most popular online platforms that regularly sell exotic wildlife, including Tokopedia, Shopee, OLX, Kaskus, Bukalapak and Jualo (Iqbal 2015; Morgan and Chng 2018; Fink et al. 2021; Nijman et al. 2021; Mutiaradita et al. 2023; Annisa and Satria 2024) for any adverts selling Prevost's squirrel. Adverts remain online, even after a sale has been made, and this allowed us to cover the period April 2021 to March 2024. The 'official' common name for Prevost's squirrel and the one that is used by the Indonesian Ministry of Forestry when allocating quotas is *bajing mandiwoi*. Occasionally *tupai belang* is used. In trade, however, the species is mostly referred to as *tupai tiga warna* or *bajing tiga warna* (also written as *3 warna*), i.e. three coloured squirrel. We used all the local Indonesian names for the species, in combination with *jual* (sale) for online searches. We noted the location of the vendor, the number of squirrels on offer, the age when given, and the asking price. Identical adverts (either posted by someone with the same username or by using identical descriptions and photographs), and vendors posting on two or more online platforms were counted only once, and re-advertisements (where the same vendor puts up the same post after a short period of absence) were not included.

Like with the physical market surveys, in September 2022 and August 2023, we extended this search, this time to eight other countries (Thailand, Japan, The Netherlands, Germany, Portugal, Sweden, UK, USA) for affirmative data on Prevost's squirrels for sale there. These searches were conducted by authors V.N., E.H., T.Q.M., J.C., B.C.R., P.S. and M.S.S. allowing us to cover a wide range of languages.

Analysis

Asking prices in Indonesian rupiah were corrected for inflation and converted to US dollars using the exchange rate for December 2023. We obtained government recommended minimum monthly wage for 2023, for each of the cities where we found Prevost's squirrel for sale, and again converted these to US dollars. Geographic distances between cities where the species was offered for sale and the nearest geographic range were measured following the shortest overland distance and where relevant, the shortest sea route (from main port to main port). A trader in Serang, Banten, offered six Prevost's squirrel that originated from Sumatra and seven from Indonesian Borneo; in this instance, we used two distances, but for all other trade the shortest distance was taken. The distance for trade in the cities within the species' native range was set at an arbitrary 25 km, as we do not expect Prevost's squirrels to occur in the city itself (as they are confined to natural forest rather than for instance city parks).

We used a Generalised Linear Model to test which factors influenced the number of Prevost's squirrels offered online. The factors considered for each city where trade was observed were (1) human population in 2020 (in millions), (2) the government recommended minimum monthly wage (in US dollars), (3) the distance to nearest wild population of Prevost's squirrel (in km, see above), and (4) whether the species was native or not to the island where it was offered for sale. We used the 'glmmTMB' function in the 'glmmTMB' package for R v 4.3.1 as this function includes several fit families that are suitable to deal with count data (Brooks et al. 2017). We tested poisson, compois, genpois, nbinom1, nbinom2 and tweedie fit families and selected nbinom2 based on the QQ plot residuals and residual vs. predicted plot from the package 'DHARMA' (Hartig and Hartig 2017).

The markets were surveyed at different frequencies (see above), and for analysis, we focussed largely on the mean number of squirrels we observed, thus correcting for the unequal sampling efforts. For analysis of all data (prices, numbers, geographic distances, minimum wages), variables were log-transformed to approach a normal distribution more closely, and we tested for equal variance allowing us to use parametric statistics. We used unpaired *t*-tests to observe any price differences between ages and numbers offered for sale within and outside the species' native range, one-way ANOVAs followed by post hoc Tukey's tests for honest difference, and Pearson's product moment correlations to test for relationships between the other variables. To test whether relatively more Prevost's squirrels were recorded within compared to outside their native range, we used chi-square tests. We present means ± 1 standard deviation of the mean. We used the Social Science Statistics software and we accept significance when $P < 0.05$ in a two-tailed test.

Results

Numbers and locations of sellers in Indonesia

We recorded a total of 284 Prevost's squirrels for sale: 115 from actual market visits and 169 found online (Fig. 2). In our physical market survey, we only detected the species for sale in Jakarta (84 individuals in three markets) and West Java (31 individuals in three markets), in all years between 2016 and 2020. On average, the species was present in 17% (range 3–44%) of the surveys from the six markets where the species was recorded. Where present, an average of 6.4 (range 1–20) Prevost's squirrels were offered for sale. Inclusion of markets that were surveyed less than 7 times resulted in one additional record (two individuals in Bogor). We did not record the species being traded in Central or East Java, Yogyakarta, Bali, or Lombok.

In terms of geographic location, the online trade in Prevost's squirrels somewhat mirrors that of the trade in physical markets. Most were offered for sale in Jakarta (54 individuals) and West Java (46), with smaller numbers in Banten (13), East Java (10), Bali (4), Central Java (3) and Yogyakarta (1).

In addition to the islands of Java and Bali, the online market survey also recorded the species for sale within its natural range on Bangka (7 individuals), on Sumatra (Jambi 10, Palembang 1, Banda Aceh 1 and Lampung 1), and on Borneo (Pontianak 2, Barito Kuala 1). For 14 individuals, it was unclear where the trader was based. In the online trade, we recorded 23 Prevost's squirrels for sale in seven cities within their natural range, and 145 for sale from 14 cities outside their range. When correcting for the number of people that live within the species range compared to outside where it was offered for sale (i.e. ~67 million in Sumatra and Indonesian Borneo vs. ~156 million in Java and Bali), there is a significant difference in the number of squirrels that were recorded ($\chi^2 = 15.43$, $df = 1$, $P = 0.0001$) but not in the number of cities where the species was offered for sale ($\chi^2 = 0.10$, $P = 0.754$).

Price relationships

We obtained 81 independent asking prices for Prevost's squirrels (mean price US\$63.28 ± 38.35), including 18 where the vendor specified the age in months. Squirrels with advertised ages between 1 and 3 months had an asking price of US\$119.35 ± 26.39, ones with advertised

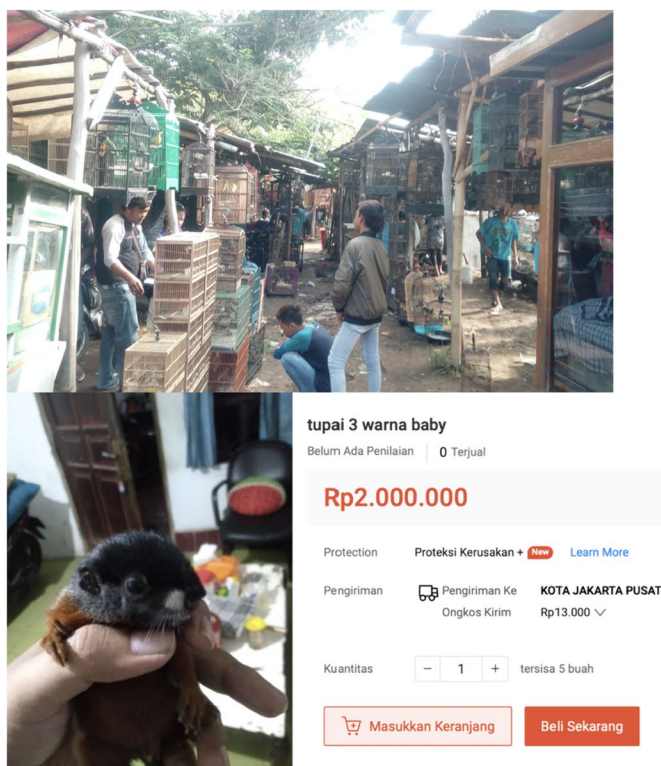
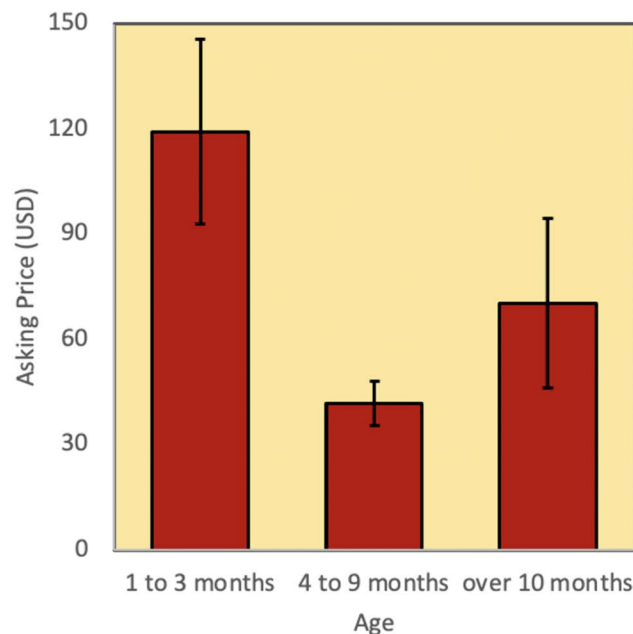


Fig. 2 Top left: animal market in Java, Indonesia. Left bottom: young Prevost's squirrel (*Callosciurus prevosti*) for sale for US\$127.31 on the online platform Shopee in November 2022; the seller is based in



central Jakarta on the island of Java, outside the native range of the species. Right: relationship between the age of a Prevost's squirrel and its asking price (mean ± sd)

ages between 4 and 9 months commended an asking price of US\$41.74 ± 6.28, and those over 10 months of age, US\$70.45 ± 24.06 (Fig. 2).

Prices between age categories were significant (one-way ANOVA $F_{2,16}=21.71$, $P=0.00003$). There was a significant difference between the very youngest and other age categories ($Q=9.57$, $P=0.00001$ and $Q=6.03$, $P=0.0016$), but no significant difference was found between the 4–9-month-old and the over 10-month-old squirrels ($Q=3.54$, $P=0.0576$).

In cities where we physically recorded only one or two Prevost's squirrels for sale prices were higher than in cities where we recorded more than ten (US\$105.03 ± 72.58 and US\$60.47 ± 35.38, respectively), suggesting rarity leads to higher prices.

The online trade showed a similar pattern as what we observed in the physical markets. Conditional on at least one detection, the number of Prevost's squirrels offered for sale in a city was positively influenced by the city's human population (Table 2), which ranged from 10.3 million in Indonesia's capital Jakarta to 0.1 million in the central Javan city of Jepara. There was a trend for it to be positively influenced by a city's recommended minimum wage (Table 2), which ranged from US\$182.90 in Pontianak, West Kalimantan, to US\$349.69 in Bekasi, West Java. Distance to the nearest wild population and whether the species was native to the island where it was offered for sale were of no influence (Table 2).

Origin

None of the traders advertised their Prevost's squirrel as being captive-bred, and this was confirmed in conversations with traders. We expect that if the species was captive-bred this would have been clearly advertised, given that young individuals that can be tamed, or indeed tamed individuals, would demand a higher asking price. This then suggests that all were derived from the wild.

Records of 140 Prevost's squirrels for sale outside Indonesia fall into two groups, differing significantly in their asking prices (t -test, $t=2.19$, $P=0.043$). The first are countries where the species is commonly offered for sale, mostly as

pairs (male/female or siblings) that have been captive-bred by the sellers, where it is legal to do so, and where prices are comparatively low. Examples of these countries are The Netherlands where we found 23 Prevost's squirrels for sale between 2019 and 2023 for US\$147 (range US\$131–158) and Germany where we found 97 for sale in 2019 to 2022, with asking prices of US\$213 (range US\$158–447). The second are countries where the species clearly (still) is a novelty species, where often single individuals are offered for sale that may have been imported or purchased rather than bred by the seller. Examples of these countries are Japan where we observed two captive-bred ones for sale in 2016 and one for sale in 2014 with an asking price of US\$2350; seven, including novel brown colour variants, in the USA (Florida, Louisiana) in 2020, 2021 and 2022 for between US\$600 and US\$3000; the UK (one pair in 2022 for US\$1220); Sweden (one pair in 2022 for US\$947); and Portugal (two in 2022 for US\$305). We also found four individuals for sale in Bangkok (200 km north of the species' natural range in southernmost Thailand) in 2021, with an individual asking price of US\$317.

Discussion

We set out to test a series of predictions concerning the trade in Prevost's squirrels (Table 2) and as predicted we found that younger squirrels, between 1 and 3 months old, were more expensive than older ones. This is similar to that found in the trade in Asian small-clawed otter (*Aonyx cinereus*) and smooth-coated otter (*Lutrogale perspicillata*) in Thailand, where age had a significant influence on asking prices (Siriwat and Nijman 2018). We did not find support for the idea that asking prices were dependent on the distance to where the animals were sourced, and prices did not reflect the purchasing power of people in the various cities. This has been found in certain other species that are traded in the wildlife markets on Java and Bali (e.g. Javan hill partridges (*Arborophila javanica* and *A. orientalis*): Nijman et al. 2020) but not in others (e.g. rufous-fronted laughingthrush (*Garrulax rufifrons*): Nijman et al. 2020). With geographic distance and purchasing power not being a barrier to trade in these squirrels, it becomes more challenging to instigate a mitigation strategy to minimise the risk of the introduction of emerging zoonotic diseases into different parts of Indonesia.

We found some support for the notion that in Indonesia, at a city level, rarity led to higher asking prices as where more Prevost's squirrels were offered for sale the mean price was lower. This would suggest that rarity, as expressed by the number of individuals that are offered for sale in a particular location, does reflect itself in asking prices (Courchamp et al. 2006; Holden and McDonald-Madden 2017) and may suggest an increase in desirability of customers to purchase

Table 2 Output of the Generalised Linear Model to test which factors were associated with the number of Prevost's squirrels (*Callosciurus prevosti*) offered for sale online

Predictor	Estimate	SEM	Z-value	P-value
Intercept	-0.141	1.636	-0.09	0.931
Distance to nearest wild population	-0.002	0.002	-1.03	0.305
Human population	0.150	0.069	2.16	0.031
Monthly minimum wage	0.008	0.005	1.77	0.077
Native to the island	-0.494	0.766	-0.64	0.519

these squirrels. Contrary to our expectation, we did not find more individuals offered for sale within the species' range (e.g. Sumatra and Borneo) than outside (e.g. Java). In fact, we found the opposite with many more for sale, especially in western Java (including Jakarta) than elsewhere. The observation that Prevost's squirrels are offered for sale by traders on the island of Bangka led credence to the suggestion that the species may be naturally present there.

While it may appear that recording of a mean number of 6.4 Prevost's squirrels per survey in the six West Javan animal markets is not high, thus suggesting that the likelihood of accidental introduction is small, these are both fully dependent on turnover (i.e. the proportion of animals that are sold in the markets over a given length of time). Furthermore, data from the online trade shows that Prevost's squirrels are offer in other parts of Java as well, and indeed in neighbouring Bali. While we do not have data on the total number of Prevost's squirrels that are offered for sale in these parts of Indonesia, their presence in a relatively large number of cities outside their native range increases the risk of accidental introduction.

Hitherto very little information has been published on the trade in Prevost's squirrels, neither from within their native range nor outside it. As mentioned in the Introduction the only quantified record of trade in the species was from the city of Medan in the 1990s and 2000s (Shepherd et al. 2004). For Thailand, Round (1990) recorded over 3000 squirrels for sale during 25 surveys in Bangkok's Chatuchak weekend market in 1989 and 1990, but two-thirds were not identified, as they were often too young. Round (1990) does not make it explicit that he observed Prevost's squirrels but he mentions the species as being illegal to sell, suggesting that indeed some of the animals on offer may have been this species. Based on online adverts and published reports, levels of trade outside Indonesia, including in other parts of the species' range (Malaysia and Thailand), appear to be low, other than in a few countries where there appears to be a tradition of captive breeding the species. We find, however, that the species is commonly traded in Indonesia, and we here discuss the legality and management implications, the risk of Prevost's squirrels establishing themselves outside their native range and disease transmission.

While the Prevost's squirrel is not included on Indonesia's list of protected species (Noerjito and Maryanto 2001), commercial legal trade in the species is very restricted (cf. Shepherd 2012). Since at least 2007 the Indonesian Ministry of Forestry has allocated a quota for harvesting Prevost's squirrels. The purpose of this harvest is for them to be used as pets and this is largely, and specifically, for export. For example, for each of the years 2007 and 2008, the legal quota was set at 150 Prevost's squirrels, but only 15 of these were intended for the domestic pet trade (Anonymous 2008). The most recent quotas from 2022 allowed 50 Prevost's squirrels

to be harvested, with only 5 being allowed to be used for the domestic pet trade (Anonymous 2022). Our observations, both in the markets and online, are not in line with these quotas. In 2022 alone, we observed over 100 Prevost's squirrels for domestic sale online and in market visits and this suggests that most, if not all, of this trade is illegal. In addition, for at least the last decade, the only province from where harvest is allowed is the province of West Kalimantan (Anonymous 2022), and it is evident, and often explicitly advertised, that Prevost's squirrels are obtained from areas other than West Kalimantan.

According to the terms and policies of the online platforms we consulted (e.g. Tokopedia, Shopee, Bukalapak and Jualo) listings explicitly forbid the sale of live animals (specified as 'no pets'; 'no animals are allowed to be sold'; 'no animals and wildlife products, including without limitations wild animals'; etc.). Some platforms, however, give the provision that the sale and purchasing of animals is allowed provided it is in accordance with Indonesia's protected species legislation. Enforcement of these policies is completely in the hands of the social media companies themselves and violations are commonplace (Iqbal 2015; Morgan and Chng 2018; Fink et al. 2021; Nijman et al. 2021).

The Indonesian government has committed itself to the prevention of the spread of invasive alien species outside their native ranges by ratifying international agreements. As a Party to the Convention of Biological Diversity (ratified by Indonesia in 1994), the country has agreed to prevent the introduction of, control or eradication of those non-native species which threaten ecosystems, habitats, or species. As part of this, Indonesia agreed to put measures in place to manage pathways to prevent their introduction and establishment. While the introduction and establishment of non-native species are often discussed in the context of introduction from other countries, within an Indonesian context with many island endemics and the fauna in the west being decisively different from those in the east, this also includes the introduction of a species from one part of the country to another. As a member of the Association of Southeast Asian Nations, the 2015 ASEAN Agreement on the Conservation of Nature and Natural Resources requires Indonesia to regulate and, as appropriate, prohibit non-native species introductions. To implement this plan, that same year Indonesia published its National Strategy and Management Action Plan for Invasive Alien Species (Yuwono et al. 2015). Some parts of this action plan are indeed appropriate for the management of all invasive alien species, but it does not really address the issues of animal movement for trade (Nijman 2022). We came across one seemingly well-planned release of two Prevost's squirrels on the island of Bangka; the animals were kept as pets, had spent some time in a rehabilitation centre and were released after veterinary inspection (Anonymous 2021). We fear, however, that many

more may have been released by well-meaning organisations and individuals, both within and outside their native range, as, for instance, has been observed with pangolins *Manis javanica*, slow lorises *Nycticebus* spp. and certain species of songbirds: Fitzsimons et al. 2011; Moore and Nekaris 2014; Prawira et al. 2018; Nijman et al. 2022; Chavez and Nijman 2024). Fear of ecological damage is what has led to non-native *Callosciurus* species being almost completely banned from import in some countries, such as Japan.

In recent years, it has become increasingly clear that there are strong links between wildlife trade and the emergence of zoonotic diseases (Greatorex et al. 2016; Tappe et al. 2019; Córdoba-Aguilar et al. 2021; Alhaji et al. 2022; Nawtaisong et al. 2022; Bezerra-Santos et al. 2023). Mazzamuto et al. (2021) discussed the parasites and the risk of zoonosis to human health of invasive populations of *Callosciurus* squirrels. They noted relative low numbers of macro parasites (ticks, intestinal worms) and inferred a low risk of macro-parasite spill over, but they found evidence of them acting as reservoirs for emerging infectious diseases, including viruses, bacteria and fungi. For example, in multiple species of German and Dutch captive squirrel populations, variegated squirrel bornavirus 1 (VSBV-1) has been found, and this has caused fatal encephalitis in both breeders and zoo caretakers. Epidemiological and phylogenetic analysis indicated a single introduction from a Prevost's squirrel. Squirrels infected are asymptomatic, but have high-viral loads, allowing for unassuming spread through bites or scratches (Tappe et al. 2019; Cadar et al. 2021). In an introduced population of Pallas squirrels *C. erythraeus* in Italy, two novel herpesviruses and one of polyomavirus were detected (Schulze et al. 2020) and an introduced population of Finlayson's squirrel *C. finlaysonii* suffered from cryptococcosis, a fungal disease (Iatta et al. 2015). These combined outbreaks led the European Centre for Disease Prevention and Control to advise against direct contact with exotic squirrels (Tappe et al. 2018). Katahira et al. (2022) studied the spill over and spillback risks of invasive Pallas squirrels in Japan and found they hosted chigger mites (*Leptotrombidium* spp.), fleas (*Ceratophyllus anisus* and *C. indages*), ticks (*Haemaphysalis flava*) and exotic lice (*Enderleinellus kumadai* and *Neophaematoponis callosciuri*). They warned that invasive *Callosciurus* squirrels can alter host-parasite relationships in an ecosystem by spreading exotic parasites and/or becoming a new (and perhaps more effective) reservoirs for native parasites. Nijman et al. (2023) discussed the risk of zoonotic diseases with *Callosciurus* squirrels being reservoirs for vector-borne diseases in wildlife markets in Myanmar and Indonesia. While we have no information on any diseases in Prevost's squirrels in the Indonesian pet trade, the prevalence of potentially emerging infectious diseases in this and other *Callosciurus* squirrels is another reason to better enforce

the restrictions that are in place within Indonesia when it concerns the trade in these species. Thus far, studies on *Callosciurus* and their diseases are largely descriptive, aiming at determining whether they are hosts for certain parasites or diseases; to reveal a potential role in parasite transmission to other wildlife and/or to humans, more detailed research is necessary (Mazzamuto et al. 2021).

The key policy highlight that emerges from this study is that Prevost's squirrels within the wildlife trade have the potential to spread infectious diseases and establish themselves as invasive species; despite their legal harvest and trade being highly restricted in Indonesia, we found hundreds of Prevost's squirrels for sale in markets and online. This suggests a lack of enforcement of existing laws and poor implementation of policies that Indonesia has agreed to as part of international agreements (CBD, CITES, ASEAN, Sustainable Development Goals) (Soehartono and Mardias-tuti 2002; Ezekiel 2018; Anonymous 2020). We urge the authorities, vendors and consumers to be more proactive in curbing the illegal trade in Prevost's squirrels and thus limiting the risk of disease transmission and of the accidental introduction on islands outside their natural range.

Conclusion

We report on the open illegal trade, both in physical markets and online, of wild-caught Prevost's squirrels, both within their native range, and even more so, outside. We point out the risk this poses for the possible introduction of this potentially invasive species on islands where it does not occur naturally, as well as the risk this trade poses for the transmission of zoonotic diseases. The reasons why the Indonesian authorities are failing to tackle these challenges thus far are numerous and complex, but it includes misconceptions and poor knowledge of basic biological issues, coupled with poor integrated planning, institutional deficiencies and possibly a lack of incentivisation on part of the authorities to take proactive action. None of these is insurmountable, and we encourage positive and proactive actions by the Indonesian authorities to address these challenges.

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Declarations

Ethics approval This study did not involve any experiments on animals or research involving human participants. In our United Kingdom and Indonesian institutes, we did not require institutional permission for observational research in animals markets; they were, however, added to Oxford Brookes University's Register of Activities Involving Animals (2016–2023). Informal discussions with traders followed the ethical guidelines proposed by the Association of Social Anthropologists of the UK and Commonwealth.

Competing interests The authors declare no competing interests.

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