LETTER

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Live reptile smuggling is predicted by trends in the legal exotic pet trade

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Abstract

Live animal smuggling presents a suite of conservation and biosecurity concerns, including the introduction of invasive species and diseases. Yet, understanding why certain species are smuggled over others, and predicting which species will be smuggled, remains relatively unexplored. Here, we compared the live reptile species illegally smuggled to Australia (75 species) to the legal trade of live reptile species in the United States. Almost all smuggled species were found in the legal US pet market (74 species), and we observed an average time lag of 5.6 years between a species first appearing in the United States and its subsequent detection in Australia. Using a Bayesian regression model, species popularity in the United States, and internationally, were positively associated with smuggling probability to Australia. Our findings give insight to the drivers of illegal wildlife trade and our predictive modelling approach provides a framework for anticipating future trends in wildlife smuggling.

KEYWORDS

alien species, biosecurity, illegal wildlife trade, pet trade, trafficking, wildlife trade

1 | INTRODUCTION

The illicit transnational wildlife trade poses a severe conservation threat, as well as a biosecurity and health risk, to trading and recipient countries (Pyšek et al., 2020; Scheffer et al., 2019). While considerable attention has focused on the scale of wildlife trade in non-Western countries (largely for consumptive practices of traditional medicine and food; 't Sas-Rolfes et al., 2019; Margulies et al., 2019), much less research has been conducted on the roles of very large Western wildlife markets (i.e., the Americas, Europe, and Australasia) for driving similar practices. This is even though Western use of wildlife has been equally long-standing (Smith et al., 2009); even for species popularly associated with non-Western practices (e.g., pangolin leather trade in the United States; Heinrich et al., 2019). Furthermore, while much of the existing focus on illegal trade of animals has focused on the smuggling of a small number of high-profile products and derivatives (e.g., ivory and rhino horns), there exists an enormous global trade in live animals—for which reptile species are particularly popular (Bush et al., 2014).

The live animal trade is of considerable concern given both accelerating biodiversity loss and the biosecurity risk from harvesting and transporting wildlife (Gore et al., 2019). Notably, the exotic pet trade is a leading

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pathway of new biological invasions for vertebrates (Lockwood et al., 2019). In addition, the global transport of live animals presents a genuine risk for panzootics, including the global outbreak of the chytrid fungi due to live trade of pet amphibians (O'Hanlon et al., 2018). Clearly, it is desirable to prevent the entry of these species prior to them causing environmental damage (Lodge et al., 2016). Indeed, prevention is recognized as the ideal and most cost-effective way to avoid new alien species establishing (Leung et al., 2012; Lodge et al., 2016).

To avoid the negative impacts caused by alien species, efforts to evaluate the invasion risk of incoming species are a biosecurity priority (Keller et al., 2007; McGeoch et al., 2016; García-Díaz et al., 2017). Risk assessments are integral in shaping the management of the import and keeping of alien species (i.e., Bomford et al., 2008; Gordon et al., 2016), yet there is a paucity of predictive research aimed at characterizing illegally smuggled species in order to preempt future threats and drive biosecurity decision-making. One reason for the lack of research on wildlife smuggling is its illicit and occluded nature, which makes it extremely difficult to observe directly (Gnambs & Kaspar, 2015). A data-driven approach to predict the identity of likely smuggled species is highly desirable (e.g., using wildlife seizure data; Hitchens & Blakeslee, 2020).

Here, we test if the popularity of exotic reptiles in the United States, and internationally, can predict the identity of reptiles smuggled into Australia (Figure 1). Australia currently imposes strict regulations on the importation of wildlife, effectively banning the import and trade of all alien reptile species (Department of the Agriculture, Water and the Environment, 2020). Yet, biosecurity records indicate a continuous stream of alien reptiles smuggled into Australia since 1999 (Henderson et al., 2011; Toomes et al., 2019). We hypothesize that the United States is the best available proxy for the "Western" live pet trade as it contributes the largest volume and most diverse set of live pets globally, has a largely unregulated reptile trade, and, importantly, keeps detailed records of wildlife imports and exports (Romagosa, 2014). Further, given the shared cultural values across many aspects of Western societies (Beck et al., 2003), we posit that species found in the US market consist of the majority of the species desired as pets in Australia (Toomes et al., 2020). Using a Bayesian regularized logistic regression model, we assessed the relationship between the probability of a reptile species being smuggled into Australia (i.e., smuggling probability) with the species' frequency in the US trade, along with other trait-, taxonomy- and trade-based covariates. Finally, we use our model to forecast priority-risk species which might be smuggled to Australia in the future.

2 | METHODS

2.1 | Data sources and explanatory variables

To identify reptile species illegally smuggled into Australia, we used a comprehensive dataset of all recorded alien vertebrate incursions to Australia from 1999 to 2016 (Toomes et al., 2019). From this dataset, we considered all records of reptiles smuggled to Australia (Appendix S1).

To represent the composition of species present in the legal "Western" pet trade, we used two US trade datasets: (1) live imports/exports to/from the United States and (2) US reptile pet store inventories. The United States is a dominant marketplace in the exotic pet trade (Harfoot et al., 2018), and places little to no legal restrictions on what species can be traded (Smith et al., 2009). The US import-export record of live animals is compiled by the US Fish and Wildlife Services under the Law Enforcement Management Information System (LEMIS; Romagosa, 2014). Unlike most countries, LEMIS records every animal/animal-derived product entering and leaving the United States, making it one of the most complete live animal import-export records of any country globally. We chose to use LEMIS records from 1999 to 2016 to match the temporal coverage of the Australian smuggling dataset. We used all legal shipments from LEMIS and ignored illegal shipments. For the second dataset, we used data collected from a web scraping effort of online US pet stores (2012-2016; Stringham & Lockwood, 2018).

We excluded native Australian species from both the US trade and Australian smuggling datasets. For each dataset, we resolved species names and higher-level taxa to the GBIF (Global Biodiversity Information Facility) taxonomic database (GBIF, 2020). This resulted in 1,445 species in the US trade and 75 species smuggled to Australia. We calculated the time lag between the year a species was traded in the US market (first year of import or export) compared to the first year the species was smuggled to Australia. See Appendix S1 for further details on data compilation methods.

We tested eight explanatory variables (i.e., covariates) in our statistical model (Table 1; Appendices S2–S5), which we hypothesized to influence smuggling probability. The first five continuous covariates are market-level indicators of abundance or popularity in the United States and international live-reptile trade: imports and exports (respectively) to/from the United States (number of individuals; from LEMIS dataset); the number of years either exported or imported to/from the United States (from LEMIS dataset); the number of listings recorded in US



FIGURE 1 The Western exotic pet trade in relation to smuggled reptile species to Australia. (a) The United States legally imports, exports, and domestically breeds millions of individual reptiles annually. Of the 1,445 species recorded in the US trade (excluding Australian natives), (b) 74 species have been illegally smuggled to Australia. Thus, all but one of the 75 species smuggled to Australia are found in legal US commercial trade (in import–export records or in pet stores). The globe in-between panels (a) and (b) represents the undocumented trade that occurs in other countries. (c) The majority of smuggled species had a time delay between when they were first traded in the United States to when they were detected as smuggled to Australia. Five species did not experience a (positive) time delay and were detected in Australia prior to being in the US market. Every species with a time lag of zero years was first traded in the United States in 1999 and first smuggled to Australia in 1999. Given both the US trade and Australian smuggling datasets commence in 1999, the zero-year time lag is most likely an artifact of record keeping and suggests these species do not have a recorded date of being imported or exported from the United States (i.e., only found in US pet stores) (Appendix S9). Thus, 68 species are shown in panel (c), where one dot represents one species. Icon colors denote the four reptile clades: gray (Crocodilia), purple (Lacertilia), pink (Serpentes), and green (Testudines). Popular smuggled species pictured in (b) include (from left to right) the corn snake (*Pantherophis guttatus*), leopard gecko: Matt Reinbold; and red-eared slider: Massimo Lazzari

pet stores (i.e., US popularity; Stringham & Lockwood, 2018); and the number of listings recorded on international online reptile marketplaces (i.e., international popularity; Marshal et al., 2020). We predicted that the more traded or popular a species is, the more likely it will be smuggled into Australia, as more popular species are generally considered desirable (Toomes et al., 2020). Second, we used the CITES listings (Appendices I, II, III) as a categorical covariate. We predicted heavily traded species faced with extinction risk (i.e., CITES listed) will be more likely to be smuggled (e.g., the Anthropogenic Allee effect; Cour-

champ et al., 2006). We used the adult mass as a specieslevel trait and predicted that size will be positively related to smuggling, as larger species are more desired as pets (Mohanty & Measey, 2019) and generally considered more charismatic (Berti et al., 2020). Finally, we included taxonomic family as a random effect because we predicted there to be differences in smuggling rates due to the desire for certain taxa, which might not be fully accounted for by other covariates in the model (e.g., Pythons are the most traded snake family; Hienrink et al., 2020). See Appendix S2 for details on compilation of explanatory variables.

Explanatory variable	Description	Hypothesized influence on smuggling	Value range: median/mean (5-95 quantile)
Exports	Total number of individuals exported from the United States	Positive	15/80,528 (0-47,649)
Imports	Total number individuals imported to the United States	Positive	77/12,297 (0-71,087)
Years	Number of years found in US import or export records	Positive	6.0/8.0 (1-18)
US popularity	Monthly average number of listings in US pet stores	Positive	0/0.15 (0-0.92)
International popularity	Monthly average number of listings from international online reptile marketplaces	Positive	0.07/0.35 (0-2.12)
Mass	The median mass (g) of a species	Positive	154/2,111 (1.4–14,735)
CITES	The CITES listing status of a species (categorical, including not listed species)	Positive with increasing protection status	-
Family	The taxonomic family of a species	Mixed, dependent on family	-

TABLE 1 Explanatory variables explored and their hypothesized influence on smuggling probability (see Appendix S2 for details on variable derivation)

Note: Each variable contained no missing data (n = 1,445) except for mass where n = 881 (see Appendix S3 for imputation details). For a visual representation of variable distributions, see Appendices S4 and S5.

2.2 | Statistical analysis

We performed a Bayesian regularized logistic regression, with "smuggled to Australia" as the binary response variable (i.e., yes or no) and the aforementioned explanatory variables. We considered taxonomic family to be a random effect (i.e., random coefficient) in our model. We imputed values for mass as some species had missing values (39% missing data). We used fivefold cross validation to evaluate the explanatory (training dataset) and predictive (testing dataset) capacities of our model and to derive coefficient estimates and predicted probabilities of each species in the dataset. To evaluate the model's fit to the data and its predictive abilities, we calculated the following diagnostic metrics on both the training and testing datasets: ROC AUC (Area Under the Receiver Operating Characteristic Curve), Bayesian p-values, uniformity of residuals, presence of outliers, dispersion, and zero inflation. A model with a ROC AUC value greater than 0.8 is considered to have excellent discrimination abilities (Mandrekar, 2010). For detailed methods on the Bayesian modelling methods and diagnostic metrics refer to Appendix S3.

To investigate "priority" risk species, we examined species with the highest predicted smuggling probability (from our model) but which, to date, have not been detected as smuggled into Australia. To identify these species, we calculated the threshold value that maximizes the kappa statistic along with its upper and lower 95% credible intervals (from cross-validation). From these thresholds, we allocated species with a predicted smuggling probability above the upper threshold a label of "high risk," above the median threshold "likely risk" and above the lower threshold "low risk" (Figure 2).

3 | RESULTS

Seventy-five (75) reptile species were reported as smuggled into Australia between 1999 and 2016 (Figure 1b). All but one of these smuggled species were also found in the legal US trade (*Astrochelys yniphora*, from 1,445 species, excluding Australian natives; Figure 1a). We observed an average delay of 5.6 years (standard deviation = 5.9 years) between being first traded in the United States and smuggled to Australia; this delay differed by taxonomic clade (Figure 1c).

Our Bayesian regularized model performed and predicted very well, with a training ROC AUC median value of .95 (standard error of ± 0.01) and test ROC AUC of .90 (± 0.03). Further, all examined diagnostic metrics indicated that the model fitted and predicted the data adequately (Figure 2; Appendix S3). Popularity in US pet stores, the number of years in the US trade, and international online-marketplace popularity had clear positive effects on smuggling probability (Figure 3a; positive 95% credible Intervals that do not overlap with zero). Of the continuous variables, US popularity had the largest influence on smuggling probability (median effect size around double that of international popularity). The number of exports and imports from/to the United States had a positive





FIGURE 2 Median predicted probability output from our Bayesian regularized model for species recorded as smuggled to Australia (n = 75) and not smuggled to Australia (n = 1,370). The middle line of each box depicts the median value while the lower and upper lines of each box depicts the 25th and 75th percentile, respectively. Red dotted lines indicate the risk thresholds for categorizing priority-risk species. Labelled species names correspond to the species depicted in Figure 4

relationship with the smuggling probability, although the effect was slightly uncertain given that their 95% credible intervals marginally overlapped zero. Adult body mass had no influence on smuggling probability.

Species listed in Appendix I of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) clearly had a higher smuggling probability compared to species not listed in CITES, after controlling for other covariates (Figure 3b). Three reptile families clearly had a higher smuggling probability (positive effects with credible intervals not overlapping zero): Elapidae, Kinosternidae, and Testudinidae (Appendix S6).

We identified 69 priority-risk species that were above the minimum threshold for being likely to be smuggled to Australia in the future (5% of eligible species; Appendix S7). One species (panther chameleon, *Furcifer pardalis*) had a predicted smuggling probability above our "high" threshold and thirteen species had a predicted smuggling probability above our "likely" threshold (Table 2; Figure 4).

4 | DISCUSSION

Western countries play a prominent role in the legal and illegal wildlife trade, particularly in exotic pet keeping (Lockwood et al., 2019). All but one reptile species recently smuggled to Australia is found in the US trade. On average, we observed that species were first smuggled to Australia around six years after first appearing in the US trade. It is our interpretation that the recent demand for illegal species has therefore originated from species already present in the Western pet trade rather than "new" emerging or fanciful species. This information can be readily incorporated by practitioners to access and anticipate risk.

Geographically distant countries are connected through the trade of their commodities, including wildlife (Fukushima et al., 2020). Here, we provide the first evidence that market-level indicators of legal wildlife trade in one country (the United States) have a strong predictive power to discern which species are smuggled illegally



FIGURE 3 Bayesian regularized model median coefficient estimates and 95% credible intervals. (a) Continuous covariate coefficient estimates. (b) CITES, categorical covariate coefficient estimates. The CITES Appendices I, II, III coefficient estimates are relative to the model intercept, representative of species not listed in CITES. Therefore, CITES Appendix I shows a clear positive increase in smuggling probability (95% credible intervals do not overlap zero) compared to species not listed in CITES (the intercept). See Appendix S6 for coefficient estimates of each taxonomic family



FIGURE 4 A subset of species with no records of smuggling to Australia but which have a high-likely predicted smuggling probability from our Bayesian regression. From left to right, row wise: *Furcifer pardalis* (Panther chameleon); *Lampropeltis mexicana* (Mexican kingsnake); *Python brongersmai* (Brongersma's short-tailed python); and *Pyxis arachnoides* (Spider tortoise). Photo of *F. pardalis* by Charles J. Sharp; *L. mexicana*: Petr Brož; *P. brongersmai*: Tontan Travel; and *P. arachnoides*: Klaus Rudloff

A.	Median predicted	r	Years traded in		International	
Species	probability	Family	the US	US popularity	popularity	CITES
Furcifer pardalis	0.97	Chamaeleonidae	18	2.5	5.5	П
Python molurus	0.82	Pythonidae	12	0.0	8.6	Π
Python brongersmai	0.67	Pythonidae	14	1.1	4.1	Π
Lampropeltis mexicana	0.67	Colubridae	18	1.1	2.8	NL
Epicrates maurus	0.60	Boidae	17	0.7	3.1	Π
Corallus hortulanus	0.54	Boidae	18	0.4	3.1	Π
Pyxis arachnoides	0.54	Testudinidae	7	0.0	0.9	I
Indotestudo elongata	0.47	Testudinidae	15	0.6	1.4	Π
Chironius carinatus	0.46	Colubridae	16	0.0	5.0	NL
Physignathus cocincinus	0.43	Agamidae	18	1.5	0.6	NL
Malacochersus tornieri	0.43	Testudinidae	16	0.5	1.2	П
Sanzinia madagascariensis	0.42	Boidae	2	0.0	2.7	I
Lygodactylus williamsi	0.40	Gekkonidae	6	0.5	2.0	I
Gonyosoma oxycephalum	0.38	Colubridae	18	1.1	1.0	NL
Vote: For CITES, roman numerals (I, II, III) represe	ent the CITES Appendix for	which the species is listed. NL stands f	or "Not Listed" in a CITE	S Appendix		

into another Western country (Australia). Demand for popular species in other countries may be fueled by global connectedness and facilitated by the Internet and related social media (Nijman, 2020). Part of global connectedness includes live species displayed in zoological parks and gardens. Interestingly, of the 69 priority-risk species identified here (i.e., not yet smuggled to Australia), 20 (29%) are currently housed in Australian zoos (Cassey & Hogg, 2015). However, household ownership of these pets is illegal due to Australia's stringent laws on alien reptile species (Toomes et al., 2020). We found that popularity on other Western international-internet markets was also positively correlated with reptile smuggling to Australia, albeit with a smaller effect than US markets. Thus, the pervasive influence of the United States in driving the reptile trade appears to be substantial-similar to many other aspects of Westernized culture (e.g., fashion, music, fast food; Tow, 2004; Beck et al., 2003).

Not only is there a demand for popular "Western" species but also there are a subset of those popular species (in the trade) that are globally threatened by the trade (i.e., CITES listed). Notably, the one species smuggled to Australia not in the US legal market (Astrochelys yniphora) is a critically endangered, CITES Appendix I member of the Testudinidae family and records indicate it is listed on international reptile markets (Marshall et al., 2020). Further, we found that tortoises (Testudinidae) had one of the highest smuggling probabilities of any family. This finding is in line with other global smuggling records where Testudinidae is the most heavily smuggled reptile family (TRAF-FIC International, 2020). Thus, in addition to the knowledge of the US market, we found it was important to consider taxonomy, CITES listings, and international market trends when identifying species at high risk of smuggling. While our results pertain directly to reptile smuggling in Australia, we hypothesize these trends are more broadly relevant to other traded taxa and other, "Western" markets.

Our model had excellent predictive discrimination, but it does not reveal any causal relationship between the United States or international wildlife markets and Australian smuggling events. Specifically, it is unclear if or how the US culture of reptile breeding and keeping is driving the Australian desire and demand for those species. We recommend that comprehensive surveys of pet owners across different countries are required to elucidate which physical traits or characteristics people find most desirable (Toomes et al., 2020). It is unknown whether the United States is directly responsible for exporting individuals that ultimately arrive in Australia. Therefore, we suggest new efforts to gather intelligence on the motivations of wildlife smugglers (e.g., interviews; Gnambs & Kaspar, 2015) to better understand the routes along which smuggling of live animals occurs and develop

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interventions around this knowledge to assist enforcement, and prevent future smuggling events (Thomas-Walters et al., 2021). Future research incorporating a criminological lens may help elucidate other patterns and drivers of live animal smuggling (e.g., Pires et al., 2021).

We identified several species common in the United States and global trade that are of high priority risk for being smuggled to Australia. We recommend these species (e.g., panther chameleon) be prioritized for risk assessments and be included in surveillance and speciesidentification training for border inspectors. Further, because the detection of smuggled species is imperfect, these species may have already been successfully smuggled into Australia but have not yet been detected nor seized by authorities (Toomes et al., 2019). Thus, it is equally important that our predictive models are available to surveillance activities for postborder biosecurity practitioners. While our predictions can be integrated to support existing biosecurity systems in Australia, the models can also be regularly updated as new information on smugglings and global market trends emerge. We suggest continued efforts to document species incursions, including smugglings, to update our understanding of risk. Specifically, we recommend surveillance of international reptile markets (e.g., Marshall et al., 2020; Stringham et al., 2021) to update the pool of species that may be smuggled along with their market characteristics.

Finally, our results provide context and guidance for other countries who seek to ban the importation of alien species to avoid their accompanying biosecurity risks (i.e., introduction of invasive species and disease). Specifically, strict bans on the importation and keeping of alien reptiles in Australia has resulted in patterns of smuggling that are explained by species popularity in the global market. In the absence of (i) the underlying motives of smugglers and (ii) quantitative information on the consumer demand for illegal species, our approach provides a path to increase the effectiveness of biosecurity efforts that seek to curb illegal wildlife trade. Considering the data we used was relatively easy to obtain or publicly available, future application to other countries and taxa is possible and highly desirable.

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AUTHOR CONTRIBUTIONS

OCS: conceptualization (lead), data curation (lead), formal analysis (supporting), investigation (lead), methodology (supporting), project administration (lead), supervision (lead), visualization (lead), writing-original draft preparation (lead), writing-review & editing (lead). PGD: formal analysis (lead), investigation (supporting), methodology (lead), software (lead), writing-review & editing (supporting). AT: conceptualization (supporting), data curation (supporting), writing-review & editing (supporting). LM: conceptualization (supporting), funding acquisition (equal), writing-review & editing (supporting). JVR: conceptualization (supporting), methodology (supporting), funding acquisition (equal), writing-review & editing (supporting). PC: conceptualization (supporting), funding acquisition (equal), writing-review & editing (supporting).

DATA ACCESSIBILITY STATEMENT

All data used in the study along with code to reproduce Bayesian regression are available from the figshare repository at https://figshare.com/articles/dataset/ Live_reptile_smuggling_is_predicted_by_trends_in_the_ legal_exotic_pet_trade/15001398.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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