Reptile smuggling is predicted by trends in the legal exotic pet trade

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Abstract

Western countries are less frequently implicated in illegal wildlife trade (IWT), contrasted with other transnational consumers, yet substantial evidence suggests that they contribute prominently. Live animal smuggling presents a suite of biosecurity concerns, including invasive species and disease risks. Here, we compared the live alien reptile species smuggled to Australia (75 species) to the legal trade of live reptile species in the United States (US) and constructed a Bayesian regularized model to predict the species most likely to be of greatest future smuggling risk to Australia. Australia has particularly strict import laws barring the entry and keeping of alien reptiles and maintains detailed biosecurity seizure records. Almost all smuggled reptile species were found in the legal US exotic pet market (98.6%), and we observed an average time lag of 4.2 years between a species first appearing in the US market and its subsequent detection in Australia. A species popularity in US pet stores, popularity on international online markets, and the number of years in US import-export records were all positively associated with the probability of species being smuggled to Australia. Our predictive model provides a much-needed early-warning guide for future biosecurity enforcement of the IWT and provides a framework for anticipating future trends in wildlife smuggling.

Main

The illicit transnational wildlife trade poses a severe conservation threat as well as a biosecurity and health risk to trading and recipient countries (Karesh et al. 2005; Scheffer et al. 2019; Pyšek et al. 2020). 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; Biggs et al. 2016; Margulies et al. 2019; Nijman 2010), much less research has been conducted on the roles of very large Western wildlife markets for driving similar practices. This is despite the fact that Western use of wildlife has been equally long-standing (Smith et al. 2009; Eskew et al. 2020); 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, rhino horn, pangolin scales) there exists an enormous global trade in live animals – for which reptile species are particularly popular (Bush et al. 2014; Auliya et al. 2016; Lockwood et al. 2019; Marshall et al. 2020).

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. 2020). Notably, the exotic pet trade is a leading pathway of new biological invasions for vertebrates (Hulme 2009; Capinha et al. 2017; 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 (Kolby et al. 2014; 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 probability of establishment, and the invasion risk of incoming species, are a biosecurity priority (Keller et al. 2007;

McGeoch et al. 2016). Risk assessments are integral in shaping the management of the import and keeping of alien species (i.e., Bomford et al. 2009; Gordon et al. 2016), yet there is a paucity of predictive research aimed at characterizing illegally smuggled species in order to pre-empt future threats and drive biosecurity decision-making. One reason for the lack of research on wildlife smuggling is due to its illicit and occluded nature, which makes it extremely difficult to observe directly (Gnambs and Kaspar 2015). Using alternative sources of data to predict the identity of likely smuggled species is highly desirable (e.g., wildlife seizure data; Hitchens & Blakeslee 2020).

Here, we test if the popularity of exotic reptiles in the United States (US), 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 of all alien reptile species (DEE 2020). Yet, biosecurity records indicate a continuous stream of alien reptiles smuggled into Australia since 2000 (Henderson et al. 2011; Toomes et al. 2019). We hypothesize that the United States (US) 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 and, importantly, keeps detailed records of wildlife imports and exports (Eskew et al. 2020). We posit that species found in the US market consist of the majority of the species desired as pets in Western countries, including Australia (Toomes et al. 2020). Using a Bayesian regularized logistic model, we assessed the relationship between the probability of a reptile species being smuggled into Australia 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 (i.e., species not reported smuggled into Australia but for which our model predicts a high probability of being smuggling). Our innovative modelling approach and resulting outcomes provide a unique early-warning capability for agencies tasked with anticipating, detecting, and preventing illegal wildlife trade.

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 US trade (*Astrochelys yniphora,* from 1,263 species, excluding Australian natives; Figure 1a). We observed an average delay of 4.2 years (standard deviation = 6.1 years) between being first traded in the US and subsequent interception in 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 0.94 (standard error of ± 0.02) and test ROC AUC of 0.88 (± 0.05). Further, all examined diagnostic metrics indicated that the model fitted and predicted the data adequately (Figure 2; Appendix S1). 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 to/from the US had a positive relationship with the smuggling probability, although their effects were slightly uncertain given that their 95% credible intervals marginally overlapped zero. Adult body mass had no influence on smuggling probability.

Species listed in Appendices I and III of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) had a higher probability of being smuggled compared to species not listed in CITES, after controlling for other covariates (Figure 3b). Two reptile families had a clear higher probability of being smuggled (positive effects with credible intervals not overlapping zero): Testudinidae and Kinosternidae (Appendix S2).

We identified 67 priority-risk species out of 1,189 species in the US trade (6%), which were not detected as smuggled to Australia but had a high probability of smuggling (Appendix S3). Two species (panther chameleon, *Furcifer pardalis*; Brongersma’s short-tailed python, *Python brongersmai*) had a predicted probability above our ‘high’ threshold of being smuggled (Table 2; Figure 4) and 17 species had a predicted probability above our ‘likely’ threshold (Table 2).

Discussion

Western countries play a prominent role in the legal and illegal wildlife trade, particularly in exotic pet keeping (Lockwood et al. 2019; Pyšek et al. 2020). Almost every reptile species recently smuggled to Australia is found in the US trade. On average, we observed that species were first smuggled to Australia around 4 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 (US) have a strong predictive power to discern which species are smuggled 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 (Tow 2004; Nijman 2020). Part of global connectedness includes live species displayed in zoological parks and gardens (zoos). Interestingly, of the 48 priority-risk species identified here (i.e., not yet smuggled to Australia), 16 (33%) are currently housed in Australian zoos (including one ‘high’ risk species: *P. brongersmai*; Cassey & Hogg 2015). However, household ownership of these pets are 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 it had a smaller effect than US markets. Thus, the pervasive influence of the US in driving the reptile trade appears to be substantial – similar to many other aspects of Westernized culture (e.g., fashion, music, fast food; Beck et al. 2003).

Not only is there a demand for popular 'Western' species, but there are a subset of those popular species (in the trade) which are globally threatened by the trade (i.e., CITES listed). Notably, the one species smuggled to Australia not in the US 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 the tortoise family (Testudinidae) had one of the highest probabilities of smuggling. This finding is in line with other global smuggling records where Testudinidae is the most heavily smuggled reptile family (TRAFFIC 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 US 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 what physical traits or characteristics people find most desirable (Toomes et al. 2020). Also, it is unknown whether the US is directly responsible for exporting individuals that ultimately arrive in Australia. Therefore, we suggest new efforts to gather intelligence into the motivations of wildlife smugglers (e.g., interviews: Gnambs and Kaspar 2015) to better understand the routes along which smuggling of live animals occurs and develop interventions around this knowledge to assist enforcement, and prevent future smuggling events (Thomas-Walters et al. 2021).

We identified several species common in the US and global trade that are of high priority risk for being smuggled to Australia. We recommend these species (e.g., panther chameleon and Brongersma's short-tailed python) be prioritized for risk assessments and be included in surveillance and identification 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 post-border 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 incursions and market global trends emerge. We suggest continued efforts to document species incursions 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). 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, which seek to curb illegal wildlife trade. Considering the data we used was relatively easy to obtain and publicly available, future application to other countries and taxa is possible and highly desirable.

Methods

Data Sources & Explanatory Variables

To identify species illegally smuggled into Australia, we used the recently compiled dataset from Toomes et al. (2019). This dataset is a comprehensive collation of all recorded alien vertebrate incursions to

Australia from 1999 to 2016. Each record contains the species, the pathway (i.e., smuggled, stowaway, or unknown), whether the incursion occurred at the Australian border or post border, and the date of the incursion. We did not consider stowaway incursions as they represent the accidental transport of species; and therefore are not actively smuggled illegal species. For the same reason, we excluded post-border at-large (i.e., found in the wild) incursions for species that have only otherwise been recorded as stowaways.

To represent the composition of species present in the 'Western' pet trade, we used two US trade datasets: (1) live imports and exports to/from the US; and (2) US reptile pet store inventories. The US 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; see Romagosa 2009 for details). Entries to this dataset are recorded by trained officers who inspect each shipment of wildlife entering or leaving the US. Furthermore, unlike most countries, LEMIS records every animal/animal-derived product entering and leaving the US. Thus, LEMIS is one of the most complete live animal import-export records of any country globally (Eskew et al. 2020), and our records span from 1999 to 2016. For the second dataset, we used data collected from a web scraping effort that spans 5 years of online US reptile 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 1,263 species in the US trade and 75 species smuggled to Australia. We calculated the time lag between the year a species was first recorded as traded in the US market (first year of import or export) compared to the first year the species is recorded as smuggled to Australia by Toomes et al. (2019).

We tested eight explanatory variables (i.e., covariates) in our statistical model (Table 1; Appendices S4 – S6), which we hypothesized to influence smuggling probability. The first five continuous covariates are market-level indicators of abundance or popularity in the US and international live-reptile trade: imports and exports (respectively) to/from the US (number of individuals; from LEMIS dataset); the number of years either exported or imported to/from the US (from LEMIS dataset); the number of listings recorded in US 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). These internet marketplaces include countries that speak English, German, French, Spanish, and Japanese (Marshall et al. 2020). We predicted that the more traded or popular a species is, the more likely it will be smuggled into Australia. Secondly, 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 (Courchamp et al. 2006). We used the adult mass as a species-level trait, by compiling mass information from several life history databases (sensu Stringham & Lockwood 2018). We predicted that size will be positively related to smuggling, as larger species are more desired as pets (Mohanty & Measey 2019). Finally, we included the taxonomic family as a random effect because we predicted there to be differences in smuggling rates due to the desire for certain taxa over others, which might not be fully accounted for by the other covariates in the model (e.g., Pythons are the most traded snake family; Hienrink et al. 2020).

Statistical analysis

We performed a Bayesian regularized logistic regression, with presence of alien species in Australia as the response variable and the aforementioned explanatory variables. Bayesian regularization allows for the inclusion of multiple covariates in a model while avoiding over-fitting by shrinking the coefficients of those relatively unimportant covariates towards zero (O'Hara & Sillanpää 2009; Hooten & Hobbs 2015). Those covariates whose posterior coefficient estimates are centered around zero contribute little to the final structure of the model. 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 (37% missing data). We used five-fold 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. We standardized all of the continuous covariates by subtracting their mean and dividing by their standard deviations prior to analyses. The standardization was independent for the training and testing datasets. 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, data imputation, and diagnostic metrics refer to Appendix S1.

To investigate 'priority' risk species, we examined the 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% quantiles (from cross-validation). From these thresholds, we allocated species with a predicted 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).

Data Availability

Data and code is available for peer review and will be publicly available upon publication.

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Author Contributions

All authors contributed to the design and revisions of manuscript. OCS conceived the idea, collected the data, and cleaned the data. OCS and PGD analyzed the data. OCS, PC, and PGD wrote the manuscript.

Tables

Table 1.

Explanatory variables explored and their hypothesized influence on smuggling probability. Each variable contained no missing data (n = 1,264) except for mass where n = 796 (See appendix for imputation details). For a visual representation of variable distributions, see Figure S1.

Explanatory variable	Description	Hypothesized influence on smuggling	Value range: Median/mean (5 – 95 quantile)
exports	Total number of individuals exported from the US	Positive	20/82,012 (0 – 44,307)
imports	Total number individuals imported to the US	Positive	71/12,546 (0 – 65,984)
years	Number of years found in US import or export records	Positive	6.0/7.2 (1 – 15)
US popularity	Number of listings in US pet stores	Positive	0/54 (1 – 336)
international popularity	Number of listings from international online reptile marketplaces	Positive	31/192 (0 – 1,580)
mass	The median mass (g) of a species	Positive	181/2,267 (2 – 15,174)
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 2.

Reptile species not previously detected as smuggled to Australia, but having a high-predicted probability of being smuggled to Australia ('high' and 'likely' species shown). For CITES, roman numerals (I, II, III) represent the CITES Appendix for which the species is listed. NL stands for "Not Listed" in a CITES Appendix.

Species	**Median predicted probability**	**Family**	**Exports from US**	**No. years traded in US**	**US popularity**	**International popularity**	**CITES**
Furcifer pardalis	0.87	Chamaeleonidae	1855	15	782	3683	II
Python brongersmai	0.73	Pythonidae	2047	11	410	3083	II
Pyxis arachnoides	0.61	Testudinidae	172	7	0	197	I
Phelsuma laticauda	0.54	Gekkonidae	331	15	202	2796	II
Epicrates maurus	0.51	Boidae	643	14	242	1901	II
Pyxis planicauda	0.50	Testudinidae	151	5	0	20	I
Malacochersus tornieri	0.48	Testudinidae	66	14	164	845	II
Indotestudo elongata	0.44	Testudinidae	37	13	173	796	II
Graptemys pseudogeographica	0.40	Emydidae	1580703	15	139	572	III
Kinixys homeana	0.40	Testudinidae	1119	16	182	75	II
Eunectes murinus	0.38	Boidae	620	15	189	1812	II
Varanus exanthematicus	0.38	Varanidae	15301	16	243	1451	II
Trioceros jacksonii	0.36	Chamaeleonidae	2045	16	653	1399	II
Chelonoidis niger	0.35	Testudinidae	2	1	0	3	I

Species	**Median predicted probability**	**Family**	**Exports from US**	**No. years traded in US**	**US popularity**	**International popularity**	**CITES**
Chironius carinatus	0.34	Colubridae	6	13	0	2833	NL
Corallus hortulanus	0.34	Boidae	1714	15	136	1376	II
Physignathus cocincinus	0.33	Agamidae	109683	15	517	579	NL
Lygodactylus williamsi	0.31	Gekkonidae	270	3	174	698	I
Lampropeltis mexicana	0.31	Colubridae	3718	15	345	717	NL

Figures

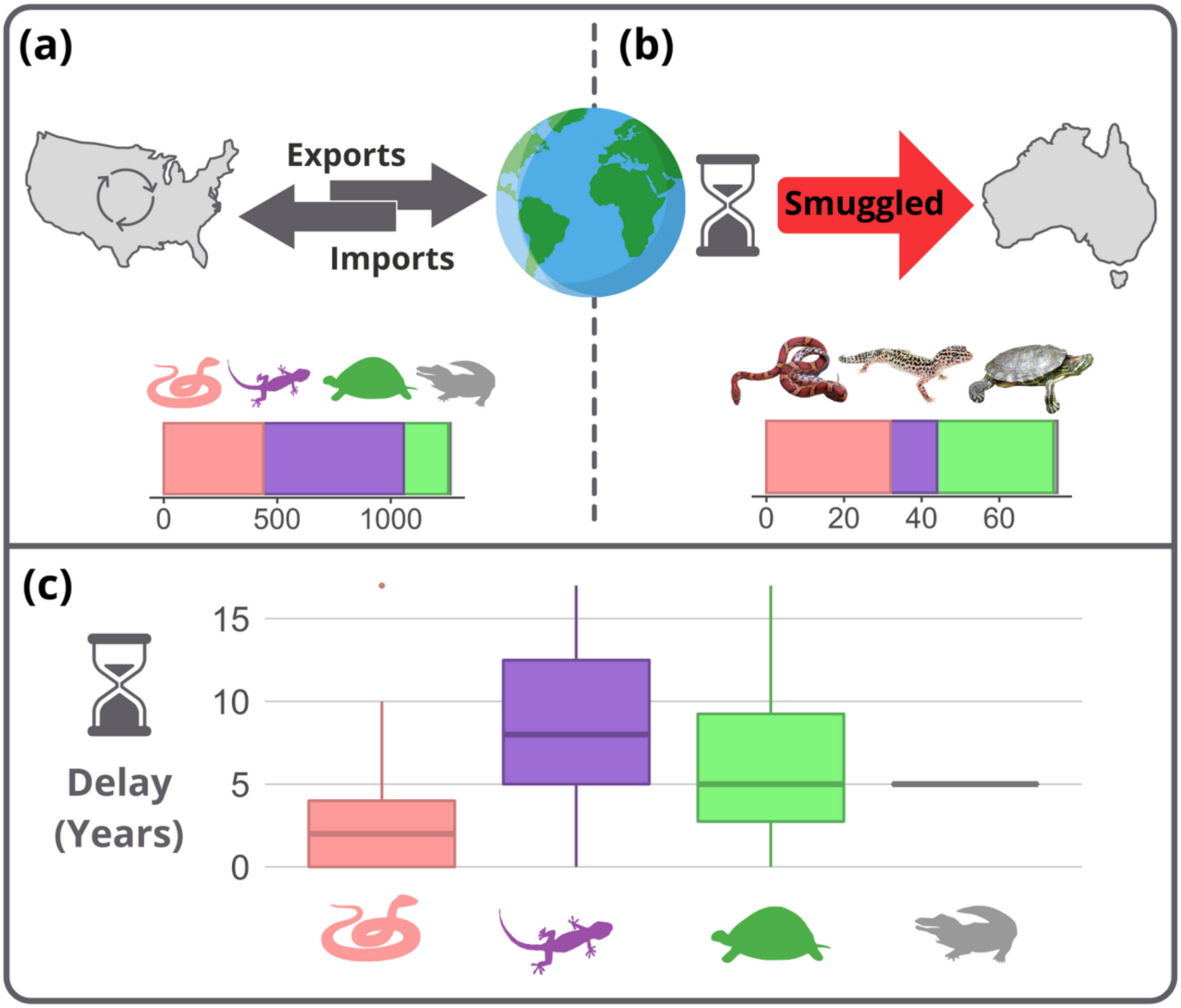

Figure 1.

The Western exotic pet trade in relation to smuggled reptile species to Australia. (a) The United States legally imports and exports millions of individual reptiles annually. Of the 1,264 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 US trade (in import-export records or in pet stores). (c) The majority of smuggled species had a time delay between when it was first traded in the US to when it was detected as smuggled to Australia. The globe in-between panels (a) and (b) represents the undocumented trade that occurs in other countries. We excluded five species from panel (c), detected as smuggled to Australia prior to being traded in the US (7% of all smuggled species; Appendix S7). Colored icons 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 (*Eublepharis macularius*), and red-eared slider (*Trachemys scripta elegans*). Photo of corn snake by: Jthatt~enwiki; leopard gecko: Matt Reinbold; and red-eared slider: Massimo Lazzari.

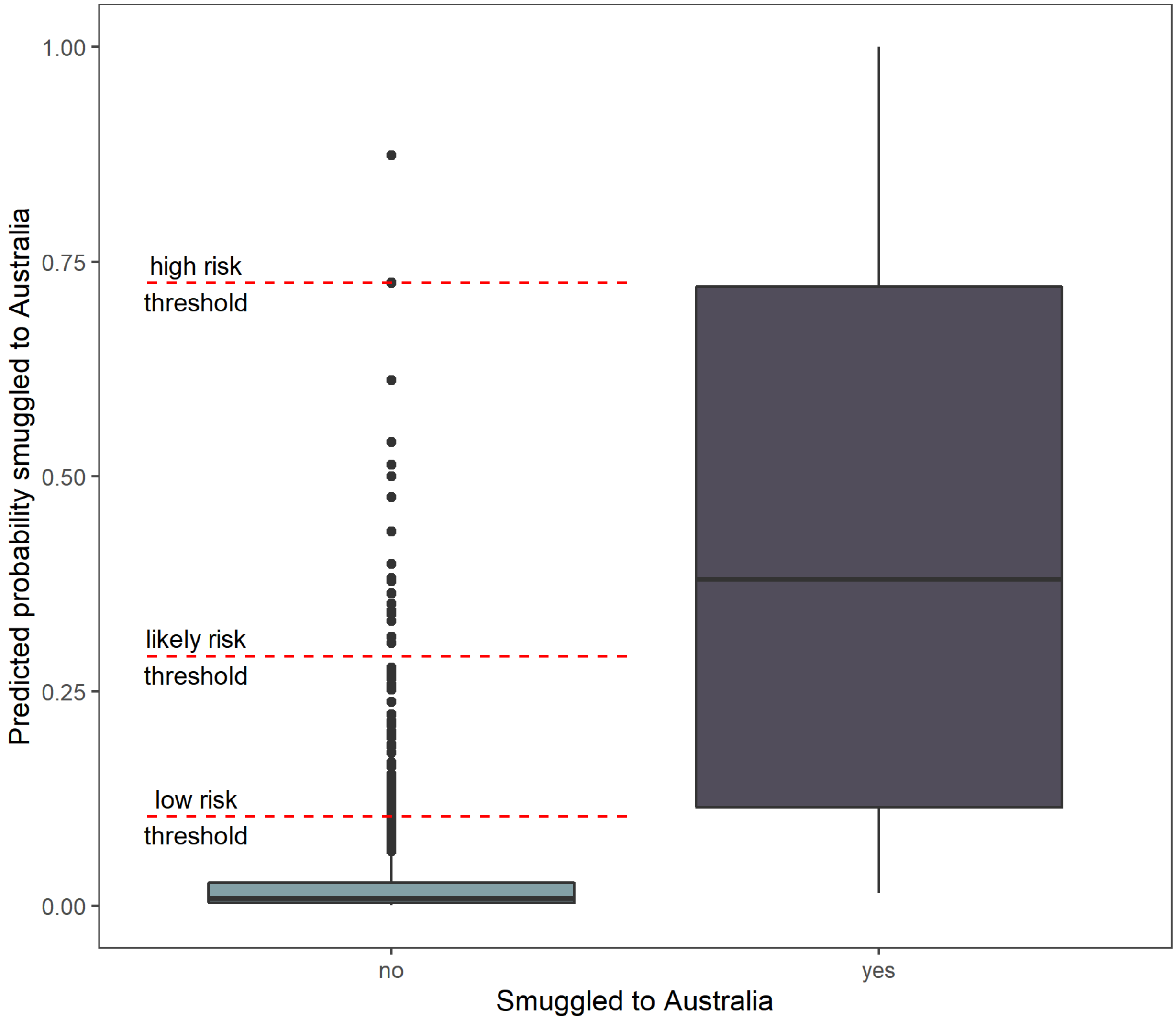

Figure 2.

Median predicted probability output from our Bayesian regularized model for species recorded as smuggled to Australia (n = 75) and not smuggled to Australia (n = 1,189). 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 species.

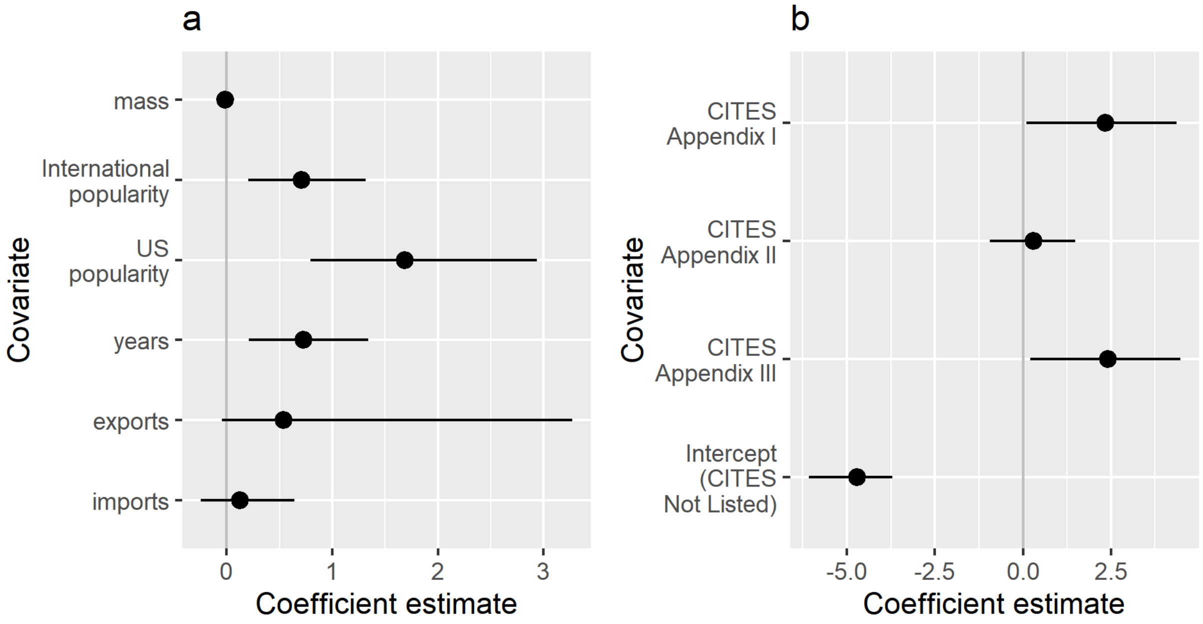

Figure 3.

Bayesian regularized model median coefficient estimates and 95% credible intervals. (a) Continuous covariate coefficient estimates. (b) CITES, categorical covariate coefficient estimates. The CITES Appendix I, II, III coefficient estimates are relative to the model intercept, representative of species not listed in CITES. Therefore, CITES Appendix I and III show clear positive increases in smuggling probability (95% credible intervals do not overlap zero) compared to species not listed in CITES (the intercept).

Figure 4.

Four species with no records of smuggling to Australia but which have the highest predicted probability of being smuggled from our Bayesian regression. From left to right, row wise: *Furcifer pardalis* (Panther chameleon); *Python brongersmai* (Brongersma's short-tailed python); *Pyxis arachnoides* (Spider tortoise); and *Phelsuma laticauda* (Gold dust day gecko). Photo of *F. pardalis* by: Charles J. Sharp; *P. brongersmai*: Tontan Travel; *P. arachnoides*: Klaus Rudloff; and *P. laticauda*: Jasen Leathers.

Supplementary Information

Table of Contents

Appendix S1.

Details on statistical model, model selection, and data imputation

S1.1 Statistical analysis

We modelled the detection of a reptile species *i* in Australia (either not detected 0, or detected 1) as a function of the continuous and categorical covariates via a Bayesian logistic regression with the following generic structure:

$$det_i \sim \text{Bernoulli}(p_i), \qquad (1)$$

$$\text{logit}(p_i) = \beta_{nc}\, I_{nc} + \beta_{eca1}\, I_{eca1} + \beta_{eca2}\, I_{eca2} + \beta_{eca3}\, I_{eca3} + \beta_{fs,i} + \sum_{j=1}^{6} \beta c_j\, X_{j,i}, \qquad (2)$$

where p_i was the probability of presence of species *i* in Australia, β_{nc} was the effect of the species not being classified in CITES, I_{nc} was a variable indicating whether the species is classified in CITES or not (1 or 0, respectively), β_{eca1} was the effect of the species being included in CITES Appendix 1, I_{eca1} was a variable indicating whether the species is included or not in CITES Appendix 1 (1 or 0, respectively), β_{eca2} was the effect of the species being included in CITES Appendix 2, I_{eca2} was a variable indicating whether the species is included or not in CITES Appendix 2 (1 or 0, respectively), β_{eca3} was the effect of the species being included in CITES Appendix 3, and I_{eca3} was a variable indicating whether the species is included or not in CITES Appendix 3 (1 or 0, respectively). $\beta_{fs,i}$ were the coefficient of taxonomic family *s* to which species *i* belongs, and β_{cj} were the coefficients of the six continuous covariates, and $X_{j,i}$ were the six continuous covariates. Note that we tested models with five and six continuous covariates (see details below). The effects of the species being included in a CITES Appendix were measured with respect to the effect of not being classified in any CITES categories, βnc. Therefore, for example, we calculated $\beta_{eca1} = \beta_{ca1} - \beta_{nc}$, and so on for the other two CITES appendices.

S1.2 Model selection

Our modelling aim was to retain the highest number possible of covariates to construct an informative model with high predictive and explanatory abilities. However, this approach runs the risk of over-fitting and covariate collinearity, which can bias the coefficient estimates and lead to a model with poor predictive power. In particular, the number of US listings and the total number of Internet listings can be correlated since the first can be thought as a subset of the latter. To account for these potential issues, we fitted nine Bayesian logistic regressions in which we varied the number of continuous covariates included and the statistical approaches for dealing with collinearity and overfitting (Table S1.A). All the statistical approaches involved different methods for defining the prior distributions and estimating the coefficients of the continuous covariates, whereas all the categorical covariates (CITES appendices and family coefficients) were always included in the models. We explored three different statistical procedures (Table S1.A): (i) multivariate normal priors ~ $MVN(0, \Sigma)$, where Σ was the covariate coefficient variance-covariance matrix. We used a relatively uninformative Wishart prior for the matrix Σ, with the variances (diagonal values) set to 10 and the covariances (off-diagonal values) set to 0 (i.e., no correlation between the covariates); (ii) Bayesian regularization, where we used a Laplace prior for the coefficients of the continuous covariates, ~Laplace(0, b), with a shared scale parameter, b ~ uniform(0, 10). This method shrinks the posterior estimate of the coefficients of those covariates that contribute relatively little to the model towards zero, resulting in a regularized model (O'Hara & Sillanpää 2009; Hooten & Hobbs 2015); and, (iii) the inclusion of indicator variables alongside the coefficients of each covariate j (O'Hara & Sillanpää 2009; Kéry & Royle 2016):

$$ind_j \sim \text{Bernoulli}(p_{kj}), \tag{3}$$

$$\beta_{kcj} \sim \text{normal}(0, \sigma_{icj}^2 = 10), \tag{4}$$

$$\beta_{cj} = ind_j \, \beta i_{kcj}, \qquad (5)$$

where ind_j indicated whether the covariate was included (1) or not (0) in each iteration of the Bayesian MCMC, p_{kj} was the probability of inclusion of covariate j, β_{kcj} was the coefficient of the covariate j regardless of whether it was included in the model during each iteration, and β_{cj} was the coefficient of the covariate j weighted by its inclusion in the MCMC iteration. The values of ind_j and p_{kj} serve to weight the importance of each covariate.

From our set of nine candidate models (Table S1.A), we selected the one that maximized the cross-validated predictive log-score (Hobbs & Hooten 2015). This scoring function is the most appropriate when the goal is to find the model with the best predictive abilities (Hobbs & Hooten 2015). To estimate the cross-validated predictive log-score for each model, we used a five-fold cross-validation approach. In each fold, we left out 30% of the dataset (testing dataset; 379 out of 1,264 observations) and estimated the mean of the log-probability of the value of the probability of detection for those observations as predicted from a model fitted to the remaining 70% of observations (training dataset; 889 observations). We did not choose observations at random to assign to the testing and training dataset given the low prevalence in the dataset that could lead to biased results. Instead, our design ensured that the proportion of 1s and 0s was the same in the training and testing datasets. Therefore, 30% of 1s and 30% of 0s were randomly assigned to the testing dataset. We repeated these procedures for each of the five cross-validations folds. Finally, we obtained the cross-validating predictive log-score of each model by summing over the five folds. The model with the highest value was considered to be the best in the set of models tested.

S1.3 Missing data imputation

We did not have information for 37% of the reptile species (468 of 1,264). We inputted these missing data within our Bayesian model via a lognormal regression, where we modelled the mass (g) of reptile species *i* as:

$$mass_i \sim \text{lognormal}(m_{\mu i}, \sigma_l), \qquad (6)$$

$$\log(l\mu_i) = \alpha + \alpha_{fs,i}\,, \qquad (7)$$

where $m_{\mu i}$ was the log mean of the lognormal distribution, σ_l was the log standard deviation, α was the mean species mass on the log scale, and $\alpha_{fs,i}$ was the coefficient of taxonomic family *s* to which species *i* belongs. We used relatively uninformative priors for $\alpha \sim$ uniform(-5, 5), $\alpha_{fs} \sim$ normal(0, σ_f^2), $\sigma_f^2 \sim$ uniform(0, 10), and $\sigma_l \sim$ uniform(1, 50). All other Markov Chain Monte Carlo methods (MCMC), including the number of chains and iterations per chain, followed those described for fitting the Bayesian model.

S1.4 Model fitting and model explanatory and predictive abilities

We fitted all the models described in the previous section using Bayesian methods as implemented in package NIMBLE (version 0.10.1) for the R statistical environment (version 3.6.0, de Valpine et al. 2017; R Development Core Team 2019). All the continuous covariates were standardized by subtracting the mean and dividing by their standard deviation. This was done independently for the training and testing dataset. We used relatively uninformative priors for all the coefficients of the categorical covariates, $\beta_{nc} \sim$ normal(0, $\sigma_{nc}^2 = 10$), $\beta_{eca1} \sim$ normal(0, $\sigma_{eca1}^2 = 10$), $\beta_{eca2} \sim$ normal(0, $\sigma_{eca2}^2 = 10$), $\beta_{eca3} \sim$ normal(0, $\sigma_{ca3}^2 = 10$), and $\beta_{fs,i} \sim$ normal(0, σ_{ff}^2), $\sigma_{ff}^2 \sim$ uniform(0, 10). For the continuous covariates, we used the priors described in the previous section. For each of the five cross-validation folds, we fitted the models using three chains with 50,000 iterations each and a thinning of 10. After confirming the successful mixing and convergence of the chains via the Gelman-Rubin diagnostic (all coefficients <1.1) and trace plots (Gelman et al. 2013; Hobbs & Hooten 2015), we discarded the first 5,000 iterations of each chain as burn-in. This protocol resulted in 45,000 draws of the posterior of each parameter in each cross-validation fold, and a total of 225,000 draws of the posterior of each parameter in our models.

Our model selection exercise revealed that a Bayesian regularized model incorporating all six continuous covariates was the best one in terms of predictive abilities (Table S1.A). We only used this model for further statistical inference. We used the same procedures described above, including the five-fold cross-validation methods, number of chains, and iterations to fit the selected model to the detection data. We evaluated the goodness-of-the-fit and predictive capacities of this model via a battery of diagnostic tests (Table S1.B). We calculated Bayesian *p*-values for the testing and training datasets in each of the five folds (Gelman et al. 2013; Hobbs & Hooten 2015; Kéry & Royle 2016). A Bayesian *p*-value compares the values of a goodness-of-fit test, the mean squared error in our case, estimated from the observed fit of the model with the value of the same test assuming that the statistical model is correct (Gelman et al. 2013; Conn et al. 2018). Non-extreme Bayesian *p*-values, i.e., > 0.05 and < 0.95, suggest an appropriate model. We estimated the Area Under the Receiver Operating Curve (ROC AUC) for the training and testing datasets in each fold (Swets 1988; Zou et al. 2007). ROC AUC scores can vary from 0.5 (predictive abilities expected by chance) to 1 (perfect predictive abilities). ROC AUC values higher than 0.7 are usually considered indicative of models with good predictive capabilities (Swets 1988). We used the library 'pROC' in R to estimate the ROC AUC scores (Robin et al. 2011).

We performed a series of posterior residual tests during each fold to ensure that our model did not suffer from statistical issues such as outliers or zero-inflation (Table S1.B). These diagnostics were based on the posterior scaled residuals, which vary between 0 and 1 and follow a uniform distribution if the model is adequate (Dunn & Smyth 1996; Gelman et al. 2013; Hooten & Hobbs 2015). The values for these tests presented in Table S1.B represent *p*-values, and very low scores (e.g., < 0.05) indicate that the model had issues for the problem being assessed. These tests were run using package DHARMa for R (Hartig 2018).

S1.5 References

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Table S1.A

Description and predictive abilities of the nine models of the detection of reptile species in Australia evaluated here. The model with the highest cross-validated score, the second one in our case (in italic, bold letters), was selected as the best model for further inference and manipulations.

Model	**Covariates**	**Method**	**Predictive log-score**
M1	6 continuous covariates Inc. US listings & Internet listings	Cross-correlation in covariate coefficients via a multivariate normal prior	29.33
M2	***6 continuous covariates*** ***Inc. US listings & Internet listings***	***Bayesian regularisation via a shared Laplace prior***	***29.39***
M3	6 continuous covariates Inc. US listings & Internet listings	Weighting of covariate coefficients via indicator variables	28.77
M4	5 continuous covariates Inc. US listings only	Cross-correlation in covariate coefficients via a multivariate normal prior	29.31

M5	5 continuous covariates Inc. US listings only	Bayesian regularisation via a shared Laplace prior	29.30
M6	5 continuous covariates Inc. US listings only	Weighting of covariate coefficients via indicator variables	29.32
M7	5 continuous covariates Inc. Internet listings only	Cross-correlation in covariate coefficients via a multivariate normal prior	29.31
M8	5 continuous covariates Inc. Internet listings only	Bayesian regularisation via a shared Laplace prior	29.28
M9	5 continuous covariates Inc. Internet listings only	Weighting of covariate coefficients via indicator variables	28.95

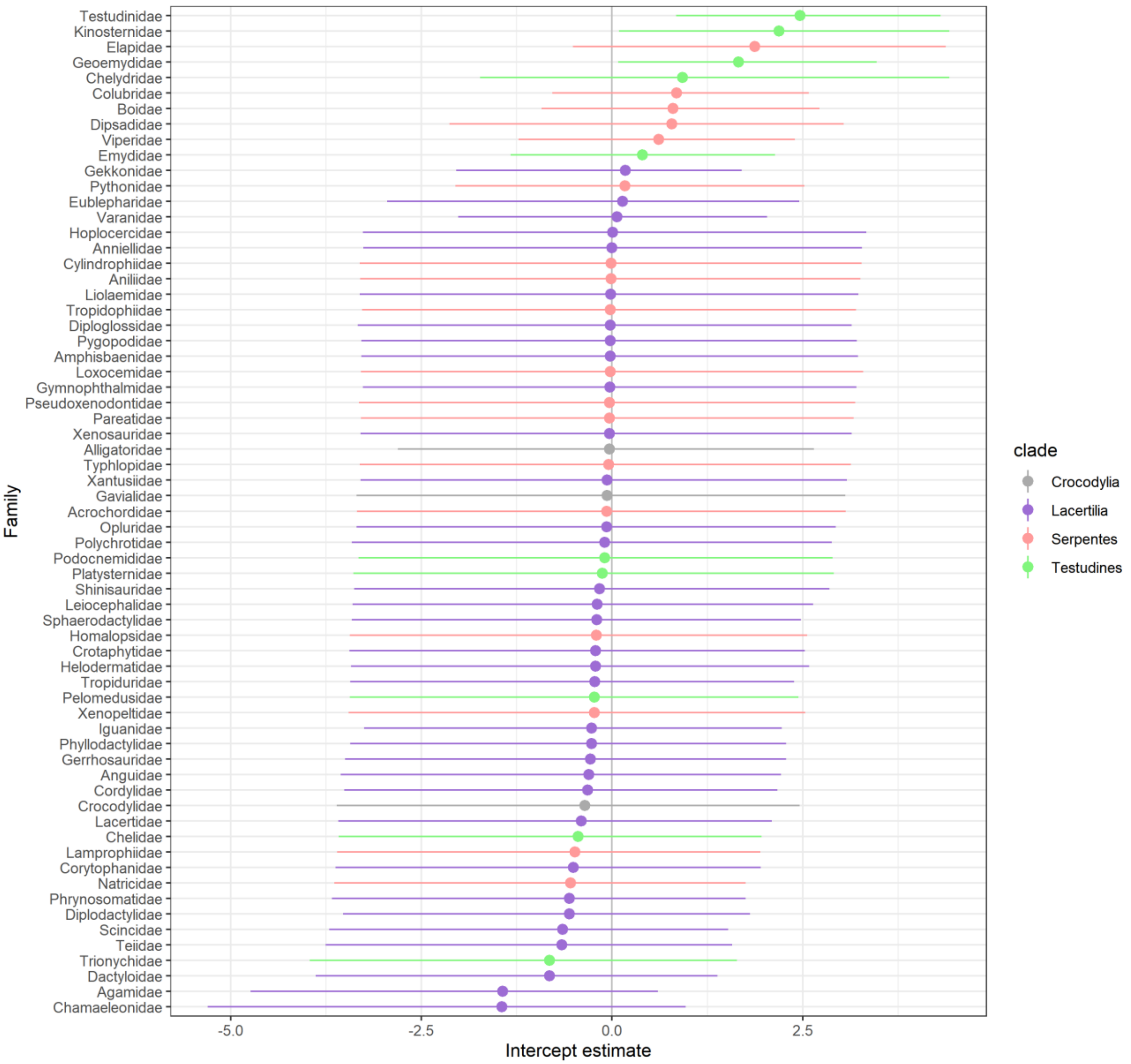
Table S1.B

Cross-validated explanatory (training dataset) and predictive abilities (testing dataset) of our Bayesian regularized model of the detection of reptile species in Australia. The values for the diagnostics of the uniformity of residuals, presence of outliers, dispersion, and zero-inflation are *p*-values and scores < 0.05 indicate a lack of model fit. All these diagnostic tests suggest that our Bayesian regularized model had good explanatory and predictive capacities.

Diagnostic test	**Training datasets** **Median ± standard error** **95% Credible Intervals**	**Testing datasets** **Median ± standard error** **95% Credible Intervals**
Bayesian *p*-value	0.50 ± 0.01 (0.49, 0.52)	0.20 ± 0.14 (0.13, 0.44)
AUC ROC	0.94 ± 0.02 (0.91, 0.96)	0.88 ± 0.05 (0.76, 0.95)
Uniformity of residuals	0.28 ± 0.25 (0.10, 0.64)	0.18 ± 0.07 (0.15, 0.29)
Presence of more outliers than expected	1.0 ± 0.00 (1.00, 1.00)	1.00 ± 0.00 (1.00, 1.00)
Dispersion	0.28 ± 0.07 (0.20, 0.38)	0.34 ± 0.24 (0.09, 0.68)
Zero-inflation	0.94 ± 0.02 (0.90, 0.95)	0.57 ± 0.43* (0.04, 0.98)

Appendix S2.

Bayesian regularized model median coefficient estimates and the 95% credibility intervals of each taxonomic family.



Appendix S3.

All 67 priority-risk species and their associated risk, predicted probability, and explanatory variables.

Species	Risk scenario	Median predicted probability	Family	Imports to US	Exports from US	No. years traded in US	US popularity	International popularity	CITES	Adult mass (g)
Furcifer pardalis	high	0.87	Chamaeleonidae	17799	1855	15	782	3683	II	42
Python brongersmai	high	0.73	Pythonidae	13669	2047	11	410	3083	II	8144
Pyxis arachnoides	likely	0.61	Testudinidae	1000	172	7	0	197	I	301
Phelsuma laticauda	likely	0.54	Gekkonidae	31902	331	15	202	2796	II	3
Epicrates maurus	likely	0.51	Boidae	1108	643	14	242	1901	II	1306
Pyxis planicauda	likely	0.50	Testudinidae	686	151	5	0	20	I	573
Malacochersus tornieri	likely	0.48	Testudinidae	4402	66	14	164	845	II	394
Indotestudo elongata	likely	0.44	Testudinidae	798	37	13	173	796	II	1150
Graptemys pseudogeographica	likely	0.40	Emydidae	16337	1580703	15	139	572	III	1477
Kinixys homeana	likely	0.40	Testudinidae	27744	1119	16	182	75	II	791
Eunectes murinus	likely	0.38	Boidae	8553	620	15	189	1812	II	85250
Varanus exanthematicus	likely	0.38	Varanidae	372240	15301	16	243	1451	II	12211

Species	Risk scenario	Median predicted probability	Family	Imports to US	Exports from US	No. years traded in US	US popularity	International popularity	CITES	Adult mass (g)
Trioceros jacksonii	likely	0.36	Chamaeleonidae	9016	2045	16	653	1399	II	31
Chelonoidis niger	likely	0.35	Testudinidae	1	2	1	0	3	I	NA
Chironius carinatus	likely	0.34	Colubridae	90	6	13	0	2833	NL	1906
Corallus hortulanus	likely	0.34	Boidae	66995	1714	15	136	1376	II	1906
Physignathus cocincinus	likely	0.33	Agamidae	1190981	109683	15	517	579	NL	162
Lygodactylus williamsi	likely	0.31	Gekkonidae	1299	270	3	174	698	I	2
Lampropeltis mexicana	likely	0.31	Colubridae	73	3718	15	345	717	NL	NA
Sanzinia madagascariensis	low	0.28	Boidae	13	0	3	0	550	I	1965
Kinixys erosa	low	0.27	Testudinidae	838	10	14	139	40	II	NA
Manouria emys	low	0.27	Testudinidae	2092	109	14	130	166	II	26000
Crotalus durissus	low	0.26	Viperidae	1108	113	15	3	254	III	1150
Apalone spinifera	low	0.26	Trionychidae	1109	695617	15	135	960	III	4765
Terrapene carolina	low	0.25	Emydidae	27	109	14	279	1573	II	372
Varanus rudicollis	low	0.24	Varanidae	5793	106	15	265	1225	II	629
Gonyosoma oxycephalum	low	0.22	Colubridae	6087	495	15	344	264	NL	5399

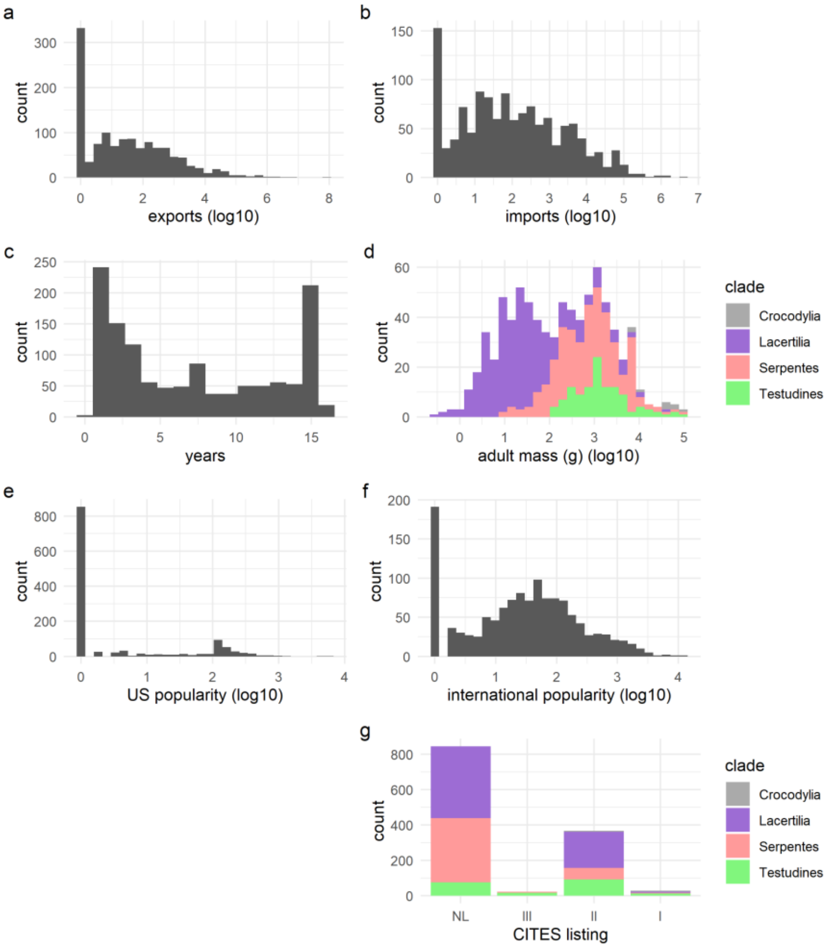
Species	**Risk scenario**	**Median predicted probability**	**Family**	**Imports to US**	**Exports from US**	**No. years traded in US**	**US popularity**	**International popularity**	**CITES**	**Adult mass (g)**
Kinosternon baurii	low	0.22	Kinosternidae	53	26847	13	135	237	NL	143
Shinisaurus crocodilurus	low	0.22	Shinisauridae	186	4	11	1	188	I	150
Acrantophis madagascariensis	low	0.22	Boidae	0	5	3	0	190	I	NA
Indotestudo forstenii	low	0.21	Testudinidae	1980	15	13	2	492	II	1503
Batagur baska	low	0.21	Geoemydidae	4	0	1	0	44	I	NA
Morenia ocellata	low	0.20	Geoemydidae	0	1	1	0	0	I	NA
Manouria impressa	low	0.20	Testudinidae	350	10	12	121	10	II	2850
Ahaetulla prasina	low	0.20	Colubridae	5394	186	15	158	942	NL	2974
Python molurus	low	0.20	Pythonidae	5473	279	10	13	2523	II	14735
Apalone ferox	low	0.19	Trionychidae	757	2645155	15	139	104	III	11872
Aldabrachelys gigantea	low	0.19	Testudinidae	1012	158	15	0	312	II	73417
Boiga dendrophila	low	0.18	Colubridae	2341	140	14	134	1094	NL	6107
Rhinoclemmys pulcherrima	low	0.18	Geoemydidae	32810	28616	15	158	285	NL	1310
Staurotypus triporcatus	low	0.17	Kinosternidae	578	2047	15	0	202	NL	4200
Staurotypus salvinii	low	0.16	Kinosternidae	902	2110	15	0	163	NL	900

Species	Risk scenario	Median predicted probability	Family	Imports to US	Exports from US	No. years traded in US	US popularity	International popularity	CITES	Adult mass (g)
Phelsuma grandis	low	0.16	Gekkonidae	31	7	3	532	1257	II	21
Varanus albigularis	low	0.15	Varanidae	13047	343	15	308	459	II	5602
Naja naja	low	0.15	Elapidae	591	74	15	0	187	II	1498
Chelonoidis chilensis	low	0.15	Testudinidae	594	52	13	0	23	II	3181
Heosemys grandis	low	0.14	Geoemydidae	455	6	8	331	30	II	NA
Gekko vittatus	low	0.14	Gekkonidae	102642	6716	15	249	650	NL	19
Anolis carolinensis	low	0.14	Dactyloidae	10274	1057094	15	253	1362	NL	2
Pituophis melanoleucus	low	0.14	Colubridae	27	4120	15	144	553	NL	6407
Platysternon megacephalum	low	0.13	Platysternidae	1020	62	7	0	105	I	NA
Rhacodactylus leachianus	low	0.13	Diplodactylidae	800	2293	15	367	838	NL	171
Phelsuma lineata	low	0.13	Gekkonidae	10299	285	15	108	1050	II	4
Micrurus diastema	low	0.13	Elapidae	10	1	3	0	2	III	NA
Kinosternon scorpioides	low	0.13	Kinosternidae	9001	9812	12	32	180	NL	266
Calabaria reinhardtii	low	0.13	Boidae	4736	126	15	149	72	II	183
Gopherus morafkai	low	0.13	Testudinidae	57	2	12	0	3	II	2357

Species	Risk scenario	Median predicted probability	Family	Imports to US	Exports from US	No. years traded in US	US popularity	International popularity	CITES	Adult mass (g)
Varanus niloticus	low	0.12	Varanidae	126742	3666	15	244	328	II	2806
Candoia aspera	low	0.12	Boidae	5110	229	15	121	140	II	384
Clelia clelia	low	0.12	Dipsadidae	91	32	9	0	1774	II	1587
Varanus jobiensis	low	0.12	Varanidae	2298	42	15	261	357	II	1091
Salvator rufescens	low	0.11	Teiidae	18825	1322	15	203	1241	II	4700
Heosemys spinosa	low	0.11	Geoemydidae	3515	45	15	0	159	II	950
Cyclemys dentata	low	0.11	Geoemydidae	14673	752	15	4	90	II	1250
Vipera ursinii	low	0.11	Viperidae	10	0	1	0	31	I	180
Micrurus nigrocinctus	low	0.10	Elapidae	5	0	1	0	3	III	729
Kinosternon flavescens	low	0.10	Kinosternidae	24	7936	12	0	71	NL	291

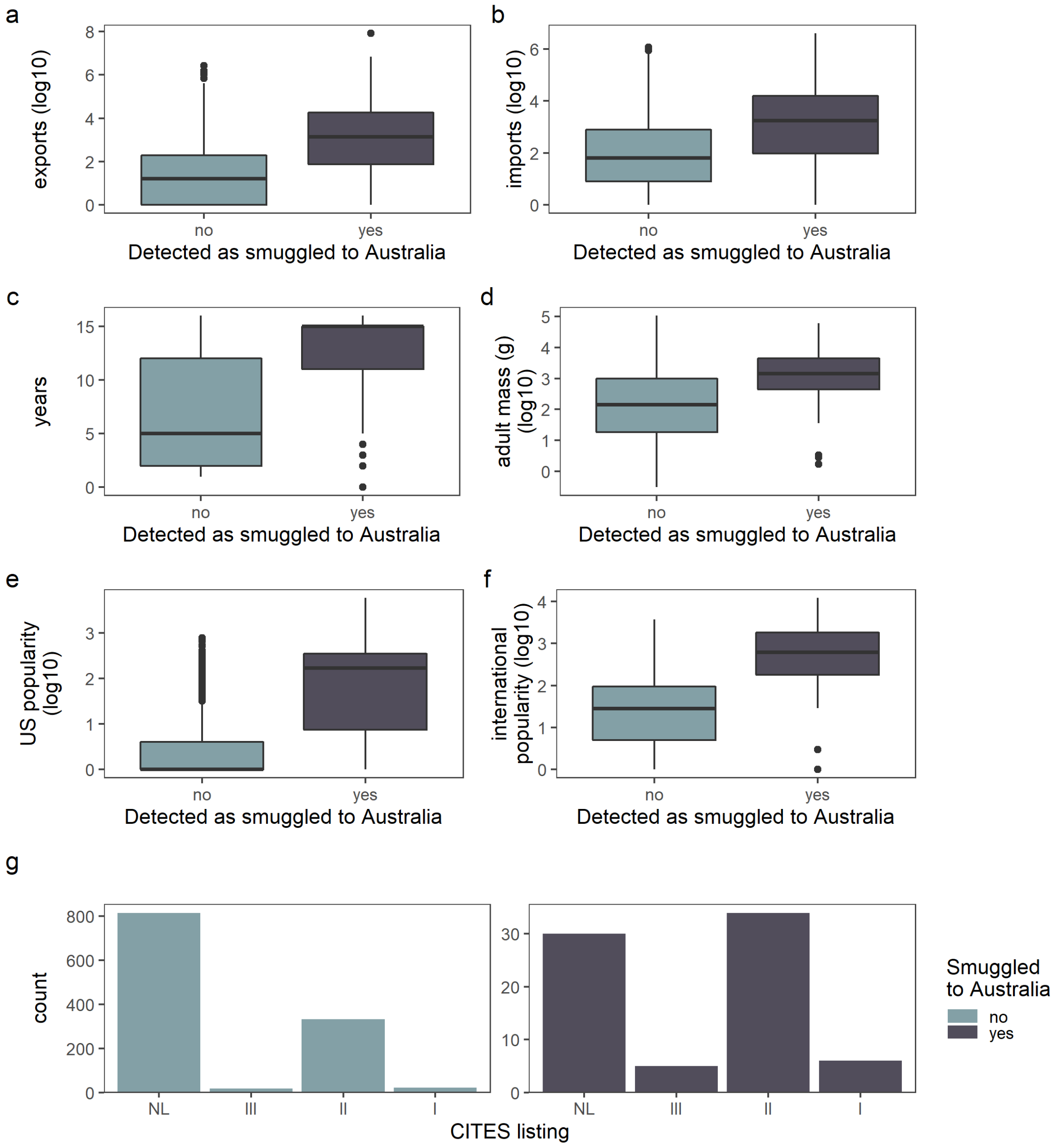
Appendix S4.

Distributions of explanatory variables: (a) number of exports leaving the US; (b) number of imports entering the US; (c) number of years in US import/export dataset; (d) adult mass (grams); (e) US popularity measured as the number of listings counted from US pet stores; (f) international popularity, measured as the number of listings counted from online international reptile marketplaces; and (g) the CITES listings. All variables that have log transformed y-axes were transformed using log10(variable + 1) to visualize zeros in the data, except adult mass where 1 was not added. Each species had no missing values for all explanatory variables (n = 1,264) except for adult mass (n = 796).



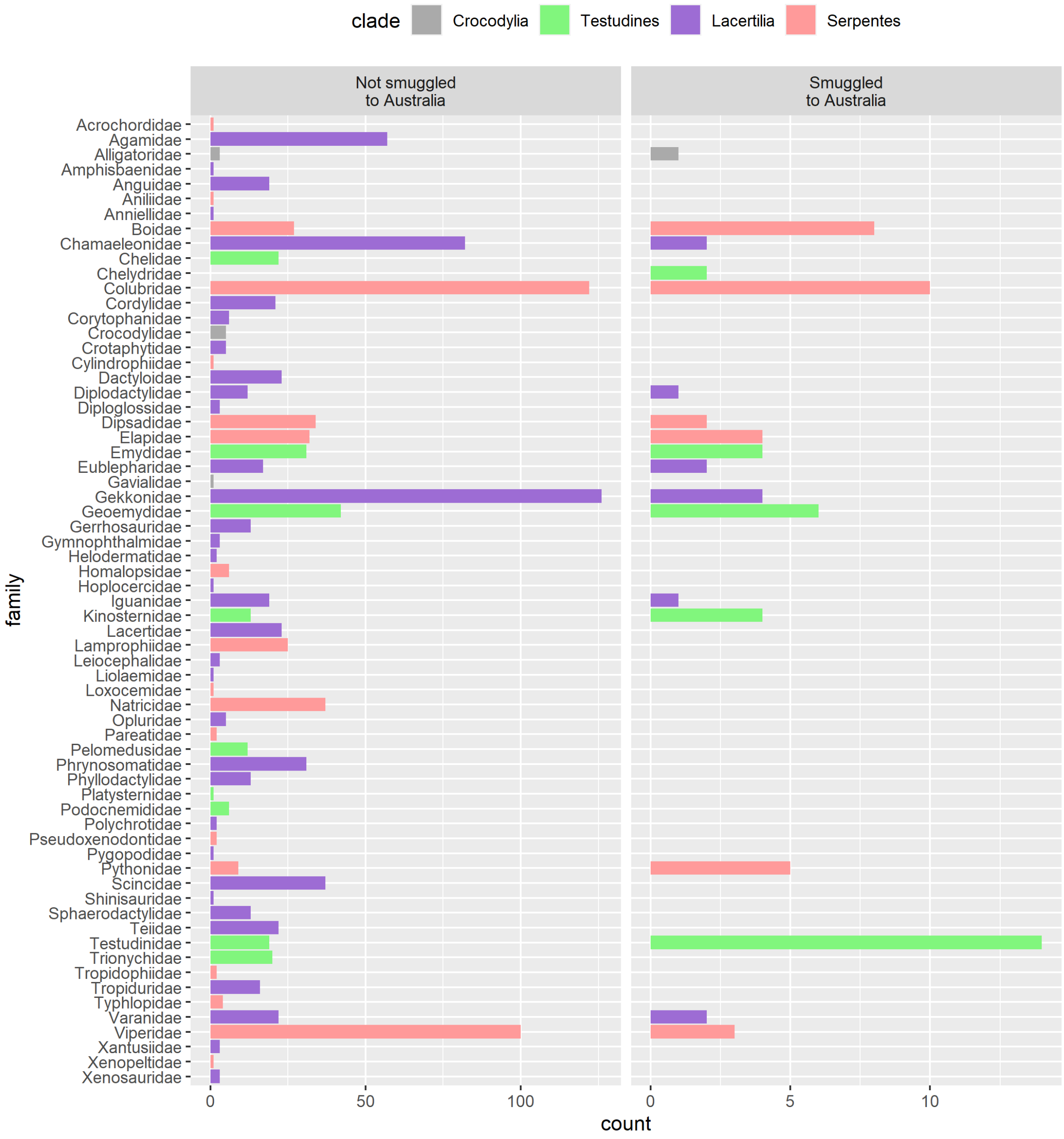
Appendix S5.

Each covariate's relationship to the presence of being smuggled to Australia (response variable). (a) Number of listings in US pet stores, (b) the number of exports from the US, (c) the number of imports to the US, (d) the number of years traded (either exported or imported) in the US, (e) the adult mass in grams, and (f) the CITES listings where I, II, and III refer to Appendix I, II, or III and NL refers to being not listed in CITES.



Appendix S6.

Number of species by family that have (right column) or have not been (left column) smuggled to Australia.



Appendix S7.

Raw data used in analyses. Data will be made public upon publication. Peer reviewers refer to file called "_reptiles_main_data_clean.csv" for data along with the data dictionary file called "data-dictionary.docx"

Appendix S8.

R code for Bayesian model. Code will be made public upon publication. Peer reviewers refer to file "BayesianRegularizedModel-Script.R".