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Pet problems: Biological and economic factors that influence the release of alien reptiles and amphibians by pet owners

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Abstract

1. The number of alien reptiles and amphibians introduced and established worldwide has increased over the last decades. The legal pet trade is now the dominant pathway by which individuals of these species arrive in their non-native locale. Despite its importance, specific factors of pet trade pathway that influence the release (introduction) of exotic reptiles and amphibians have not yet been examined.
2. We set out to identify broadscale and easily measured biological and economic factors that influence the release of these exotic pets by their owners. We hypothesize that biological factors reflect the cost of care, and economic factors reflect the value that owners place on their pet, both of which can influence the probability when a pet is released. We collected life history and economic data on the 1,722 species of reptiles and amphibians sold within the US as pets over the last 18 years. We also compiled a list of pet trade-attributed releases in the US (i.e., all free-living species regardless of whether they successfully established). We used boosted regression trees to correlate species release status with their life-history traits and economic attributes (r^2 = 0.51, AUC = 0.89).
3. We found that species with a high probability of being released were imported at higher quantities over our period of record, have a relatively large adult mass and commanded cheaper retail prices. The number imported and price interacted with longevity and adult mass to produce nonlinear increases in release probability. The most important interaction revealed that large-bodied species imported in high quantities have a three times higher release probability compared to large-bodied species imported in lower quantities.
4. *Policy implications*. Our results provide guidance towards targeting exotic pet reptile and amphibian species that are at a high risk of being released. Species that are both prevalent in the pet trade and large-bodied or long-lived have the highest probability of being released. This will aid in developing education and policy solutions aimed at decreasing the rate at which these pets are released, thus curtailing the invasion process before these species can establish and impacts can occur.

KEYWORDS
alien species, amphibians, exotic pet trade, introduction probability, introduction stage, invasions, pet releases, reptiles

1 | INTRODUCTION

Invasive reptiles and amphibians impose severe ecological and socio-economic costs including sometimes driving entire suites of native species towards extinction (Shine, 2010; Wiles, Bart, Beck, & Aguon, 2003). Over the past two decades, the trade in "exotic" pets has become the main source of alien reptile and amphibian species worldwide (Capinha et al., 2017; Kraus, 2009; Krysko et al., 2011). Exotic pets are species without a long history of domestication that are legally captured from their native range or bred within facilities and sold to consumers as household companions. Individuals sold as exotic pets are never intended for release; however, the regular observation of traded species as free-living suggests that a nontrivial fraction is released (Hulme, 2015). These released individuals then have the opportunity to establish a local population, with some further probability of an established population imposing negative impacts on co-occurring native species (Blackburn et al., 2011). Despite release being the initiating step of invasions, we know very little about the process by which exotic pets are released, in large part because pet release events are geographically localised and are known to be rare relative to the number of people who own exotic pets (Strecker, Campbell, & Olden, 2011). Add to this the difficulty of documenting the dynamic composition of the exotic pet market (Romagosa, 2014), and it becomes clear that the task of connecting trade, species life history and consumer behaviour to the occurrence of free-living pet reptiles and amphibians is a formidable challenge. Here, we generate hypotheses about how these species' biological traits, and the economic factors related to their trade, influence the release decisions of pet owners. We test these hypotheses by combining pet market data with in-depth records of documented released free-living reptiles and amphibians within the United States (US).

Research on invasion vectors and pathways makes clear that the suite of species transported via human actions is set by the interplay of socio-economic factors and species' biology (Essl et al., 2011; Hulme et al., 2008). One of the primary filters (or barriers) that alien species must transit early in the invasion process is being released as free-living within a non-native environment. In the pet trade pathway, release occurs either when the wholesaler or consumer fails to keep the individual in a secure enclosure (escape) or when the owner (a consumer or the wholesaler) purposefully removes the individual from captivity and allows it to become free-living (Su, Cassey, & Blackburn, 2016; Vall-llosera, Woolnough, Anderson, & Cassey, 2017). Since the pet trade pathway is quite distinct in the degree to which human behaviour influences the release event itself, we should expect that drivers of release are specific to this pathway (Hulme et al., 2008). For example, smaller-bodied cargo hitchhikers may be more likely to be released (accidentally) because they are more likely to go undetected. However, the reverse relationship may be true for the pet trade pathway given that larger-bodied species tend to be released more often due to them outgrowing their housing (termed "tankbusters" for fish: Holmberg et al., 2015). Thus, independent analyses of release pathways are imperative to producing meaningful insights for policy development (Hulme et al., 2017).

Despite the importance releases play in the invasion process for the pet trade pathway, most of the research to date has focused on the factors influencing the establishment of exotic pet populations and not on the factors related to their initial introduction (or release; Bomford, Kraus, Barry, & Lawrence, 2009; Fujisaki et al., 2010; Mahoney et al., 2015; Van Wilgen & Richardson, 2012). The

TABLE 1 Biological and economic factors hypothesized to influence the probability that a pet reptile or amphibian will be released as free-living by their owners. Sample size represents the number of species that have data for the variable (out of a total of 1,722 species)

Name	Description	Sample size	Expected effect on release probability
Life history			
Adult mass	Mean body mass of adults (g)	1,115	↑
Longevity	Maximum number of years known to survive either in wild or in captivity	909	↑
Reproductive output	Number of eggs per year, calculated by multiplying clutch size by clutch frequency	748	↑
Economic			
Quantity imported	Total number of live individuals imported into the US (designated for the pet trade) from 1999 to 2013	1,426	↑
Price	Five-year median of the retail price of a species (US$)	627	↓
Time on market	Number of years that a species was available for sale on the pet market (from 1 to 18 years)	1,722	↑

few published studies on pet species release are lacking in both taxonomic and analytical breadth (e.g., Duggan, Rixon, & MacIsaac, 2006; García-Díaz & Cassey, 2014; Su et al., 2016; Tingley et al., 2010). Consequently, the release stage is frequently ignored in risk assessment (Leung et al., 2012), even though there is considerable evidence that if alien species are not released, or are released in small enough numbers, they are far less likely to become established (Cassey, Delean, Lockwood, Sadowski, & Blackburn, 2018; Lockwood, Cassey, & Blackburn, 2005).

Here we seek to close this research gap by exploring the ability of biological and economic drivers to explain releases of pet reptiles and amphibians (Table 1). For biological drivers, we hypothesize that the probability of release will increase when there is a mismatch between the perceived and actual level of care needed to maintain the individual in captivity. We expect that well-meaning consumers purchase a pet but find it difficult to care for it over the long term, and that some fraction of these owners will choose to release their pet rather than sell or euthanize it. We posit that care costs will be higher for species that grow to large adult sizes, live for a long time and are capable of producing many young while in captivity. For economic drivers, we hypothesize that the more abundant and less expensive a species within the pet market, and the longer the species remains on the market, the more likely the individuals of this species are to be released. Owners may place less value on low-cost pets and therefore be more likely to release them when care becomes costly or inconvenient. Furthermore, all else being equal, the probability that at least one individual of an exotic pet species will be released will increase if the species is commonly sold to consumers, some fraction of which will resort to release when the pet is no longer wanted. By attempting to quantify the factors related to the release of exotic pets, we seek to help guide efforts aimed at curbing pet animal releases.

2 | MATERIALS AND METHODS

2.1 | Pool of species available for purchase as pets

We identified the range of species that are available for purchase as pets in the US by combining two data sources. The first is import records kept by the US Fish and Wildlife Service (Law Enforcement Management Information System, LEMIS; see Romagosa, 2014 for more details). These data are collected by trained inspection agents at airports across the US. We focused our analysis on the conterminous US and therefore excluded import records from Hawaii, Alaska and US territories. LEMIS data from 1999 to 2016 indicated that 1,613 reptile and amphibian species were imported into the US for the pet trade.

Our second data source was a list of species available for purchase on highly trafficked nationwide internet vendors from 2012 to 2016. We expected this inventory to overlap substantially in species composition with the LEMIS data. However, the web retailer sites also include species that are bred domestically and thus serves to expand our pool of species that had the opportunity to be released by pet owners. The vendors we chose to include in our survey are the top three most trafficked reptile and amphibian internet-based pet stores, each of which offers to ship individual pets to any consumer in the conterminous US. From these online pet retailers, we collated 94,230 unique individual pet listings representing 652 species (see Supporting Information Data S1 for details on our web-based data collection protocol).

2.2 | Variables that influence release

Next, we gathered information on biological factors that we hypothesized to be related to release probability (explanatory), which included mean adult body size (grams), mean reproductive output (eggs/year) and maximum longevity (years; Table 1). We expect that as each of these biological factors increases in magnitude, the incurred costs of care will also increase, thus increasing release probability. We collected this information from five published databases of vertebrate life-history traits (see Supporting Information Data S2 for details on compiling databases). Additionally, following Holmberg et al. (2015) we compared the difference between age and body mass at time of sale (retail size and age) with maximum age and adult body mass for species appearing on the web vendor sites (see Supplemental Information Data S4 for details on estimating age and mass at sale). Data coverage for maximum longevity and adult mass was substantially higher than retail mass and age, and the two measures were highly correlated (Supporting Information Data S3). Thus, we only included maximum longevity and adult mass per species in the boosted regression tree (BRT) model described below.

For the economic explanatory factors, we calculated the length of time that each species appeared in the US pet market by tallying the number of years each species was listed at least once across any of the three websites and/or within the LEMIS data. We calculated the number of imports for each species by summing across all years the number of live individuals designated for the pet trade in the LEMIS data (available for 1999–2013). We also estimated the price that an individual of each species commands on the retail market. We collated price information from all web listings per species, corrected all prices to represent December 2016 US$ and calculated the median of this distribution (Supporting Information Data S1).

2.3 | Testing for release patterns

We compiled a list of documented released (also known as introduced or free-living) exotic reptiles and amphibians primarily using Kraus (2009), which is the most comprehensive dataset of releases available on these taxa for the US. We only included species from Kraus (2009) if he listed them as having arrived in the US via the pet trade. Corresponding to the temporal span of our species pool, we only recorded as "released" species that Kraus indicates as having been observed as free-living after 1999. Because Kraus (2009) only had access to information up to about 2008, and to ensure comprehensive accounting of released species, we included species recorded as free-living from 1999 to 2016 within EDDMapS (2012; www.eddmaps.org). EDDMapS is a citizen science effort to provide real-time information on alien species occurrences across the US, where each listing is verified by taxonomic experts. There were 114 more species recorded as released from EDDMapS that were not in Kraus (2009) within our period of record. We excluded all recorded releases from Hawaii and Alaska to match our geographical scope of species availability (above). Note that we included species as "released" regardless of whether they have now, or ever will, establish self-sustaining populations in the US. Our interest is with the set of pet species that were released or escaped from captivity regardless of their long-term fate once free-living. This effort resulted in 126 species recorded as free-living somewhere in the conterminous US between 1999 and 2016. We designated these free-living species as "released" in our analyses below, and the species that were not recorded as free-living to be "not-released" (our binary dependent variable).

We used BRT to explore the relationship between our explanatory variables and the release status of reptiles and amphibians sold as pets in the conterminous US. BRT is a machine learning technique that can fit complex nonlinear relationships and handle different types of data all while potentially yielding higher predictive performance than traditional statistical models (Elith, Leathwick, & Hastie, 2008; see Supporting Information Data S5 for BRT parameters used and testing of simpler models). Our reason for choosing BRT over more traditional statistical methods such as GLMs is its ability to accommodate for missing data. While we used the most up-to-date databases (to our knowledge) to compile life-history traits, there were still missing data for all traits (Table 1). The BRT algorithm handles missing data by skipping the node with missing data during tree building (i.e., data are not imputed, but rather not included; Elith et al., 2008). BRTs were modelled in R v. 3.3.1 using the packages *gbm* v. 2.1. and *dismo* v. 1.1.

To assess phylogenetic correlations between species (i.e., Allen, Street, & Capellini, 2017; Capellini, Baker, Allen, Street, & Venditti, 2015), we performed two additional BRT models that included taxonomy (Family and Order) as a proxy for phylogeny (i.e., Schmidt & Drake, 2011; Van Wilgen & Richardson, 2012). This analysis does not directly measure phylogenetic correlations (e.g., Pagel's λ), which is a shortcoming of machine learning techniques in general (Supporting Information Data S6). Thus, we recommend that methods be developed to incorporate phylogenetic information into machine learning techniques including BRTs. With this caveat, from our analysis we found little evidence for a phylogenetic signal in release probability (Supporting Information Data S6), and given that taxonomy or phylogeny alone does not reveal which life-history traits are important predictors of release, we focus our interpretation of results below on the BRT without taxonomy.

To evaluate the performance and fit the BRT model, we used two metrics. First, we calculated the area under the receiver operating characteristic curve (AUC) for both the training (all data) and cross-validated models (average of all cross-validated data folds). Second, we calculated r^2 (percent deviance explained) for both the training and cross-validated models.

To explore how each explanatory variable influenced release probability, we examined four different metrics. First, we calculated the relative contribution metric for each explanatory variable, calculated as the number of times a variable is selected for splitting a tree, weighted by the improvement resulting from that split, averaged over all trees. Second, we generated partial dependency plots to visualize the relationship between each explanatory variable and release probability. Third, for each explanatory variable, we measured the magnitude of its influence on release probability, calculated as the range (max–min) of the values in the partial dependency plots. We termed this value Δ *P* (release), which is essentially a measure of effect size. Finally, we examined the relative strength of variable interactions by calculating the interaction size between explanatory variables (values near zero represent negligible interactions) and visualized these interactions in heat maps (Elith et al., 2008).

3 | RESULTS

Of the 1,722 species recorded either in LEMIS or on the websites, Lacertilia (lizards) were the group with the most species for sale (739 species), followed by Serpentes (snakes) with 490 species (Figure 1a). Over half of the species (1,106) were available on the market for ≤5 years (Figure 1b), while ~10% of species were available for the

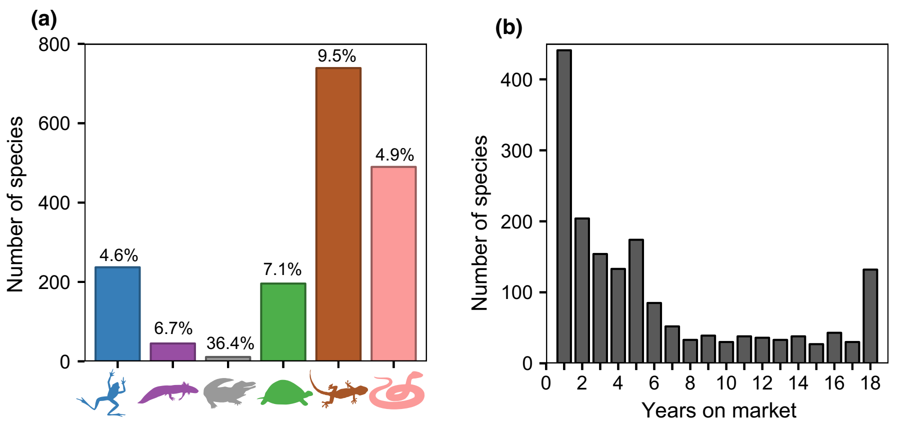

FIGURE 1 (a) Species for sale in the US exotic pet market by taxonomic group. The groups in order from left to right are: Anura, Caudata, Crocodylia, Testudines, Lacertilia and Serpentes. The percentages of species in each taxonomic group recorded as released are listed above each bar. (b) Number of years species were available for purchase within the US exotic pet market

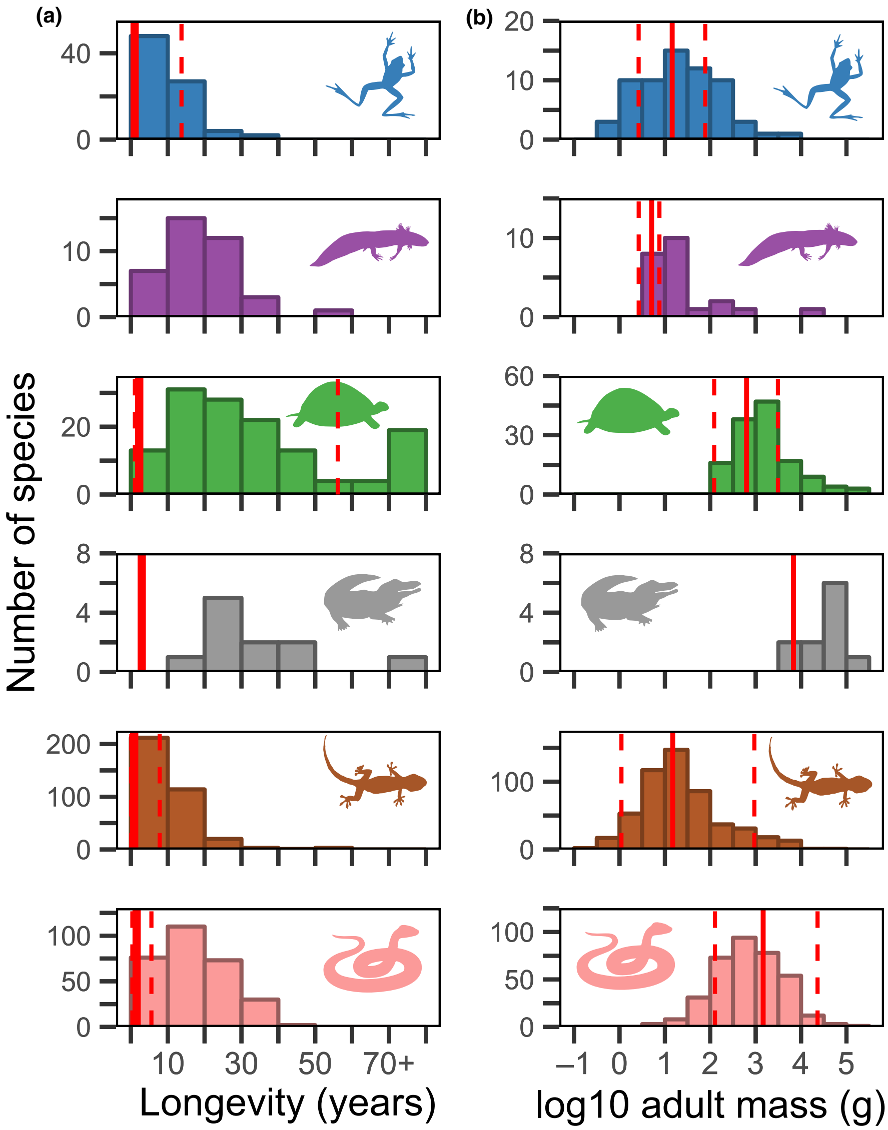

FIGURE 2 Comparison of retail age/size (vertical lines) and longevity/adult size (histograms) for each taxa. (a; left column) Longevity of species sold on the US exotic pet market by taxonomic group. (b; right column) Adult mass of species sold on the exotic pet trade by taxonomic group. Vertical solid lines indicate the median retail age (a) or retail mass (b) of all species in the specified group. Dashed vertical lines represent the 5th and 95th percentiles of retail age (a) or retail mass (b). Note for Caudata, there were no data for retail age, and for Crocodylia the retail mass was recorded for only one species, hence no visible percentile lines

full duration of this analysis, 18 years. Most web listings sold pets for under $100 although some species commanded substantially higher prices (Supporting Information Figure S1). For all taxa, the age at the time of sale (retail age) was markedly less than the species longevity (Figure 2a). A similar trend was observed for retail mass and maximum adult mass (Figure 2b).

The BRT was effective at explaining release status, with a cross-validated AUC score of 0.89 and a r^2 of 0.51. As anticipated, the AUC and r^2 are somewhat higher for the training data (AUC of 0.94 and r^2 of 0.66), since overfitting is likely without cross-validation.

Three variables had the largest effect on release probability: quantity imported, price and adult mass with a ΔP (release) of 48, 23 and 21 percentage points respectively. In terms of model fit, these same variables had the largest relative contribution to release probability (ranging 17%–30%; Table 2). The three other factors explored, time on market, longevity and reproductive output, had less of an effect on release probability and model fit.

Partial dependency plots showed that quantity imported, longevity, reproductive output and time on market had a positive relationship with release probability, whereas price had a negative relationship (Figure 3). Adult mass had an unequal "U"-shaped relationship with release probability, where intermediate values saw the

TABLE 2 Results from boosted regression tree model. $\triangle P$ (release) is a measure of the effect size of the variable and is calculated as the range of the partial dependency plots (Figure 4). Relative contribution is a measure of variable fit and is scaled so that the contributions of all variables adds up to 100%, where higher numbers indicate stronger contributions

Variable	$\triangle P$ (release)	Relative contribution (%)
Quantity imported	0.48	29.7
Price	0.23	22.1
Adult mass	0.21	17.2
Time on market	0.10	8.5
Longevity	0.09	11.5
Reproductive	0.04	11.0

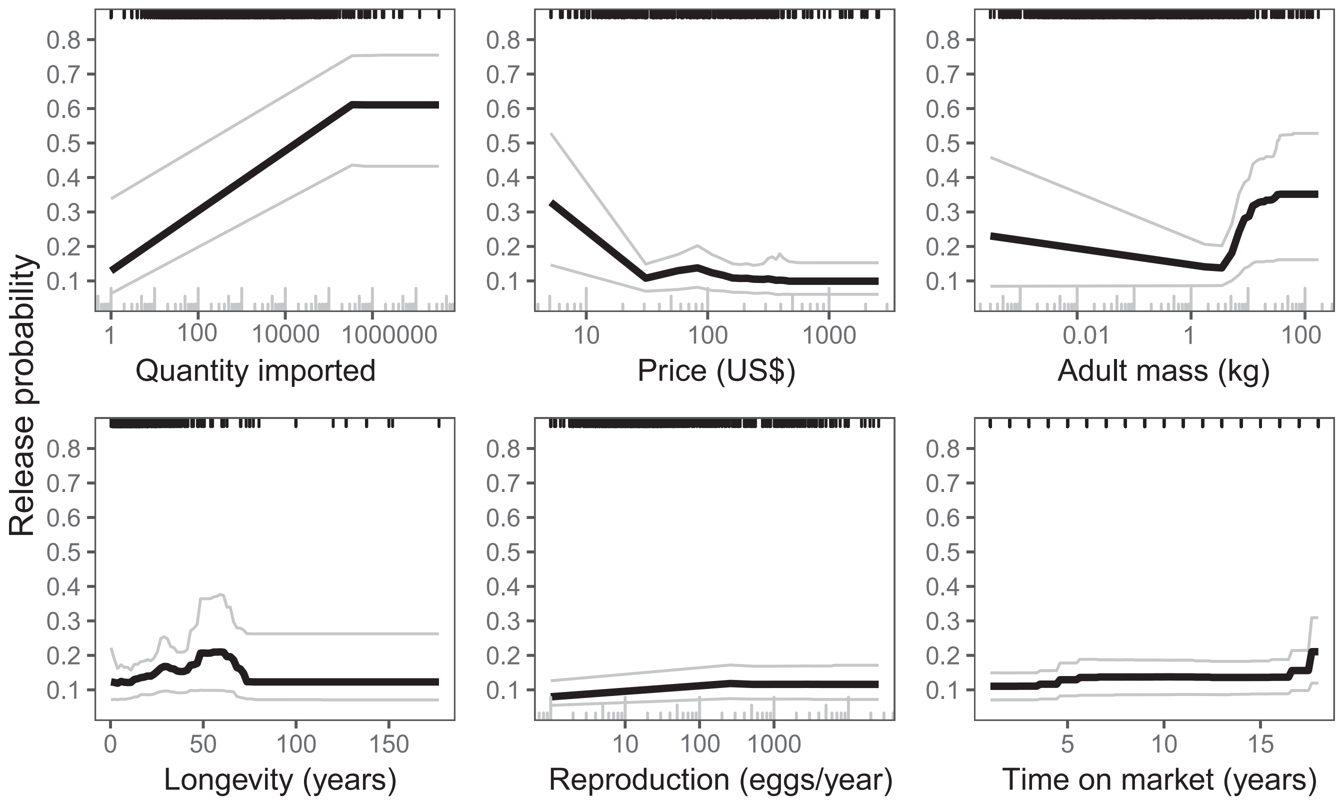

FIGURE 3 Partial dependency plots showing effects of biological and economic factors on release probability for exotic pet reptiles and amphibians in the US generated from our boosted regression tree analysis. Partial dependency plots show the effect of a given explanatory variable on release probability, while holding the effects of other explanatory variables at their average. We used 500 bootstrap replicates to calculate the 95% confidence intervals, depicted in grey. Note that several of the x-axes are on a $\log_{10}$ scale. Across the top of each plot is a rug plot showing the distribution of data points

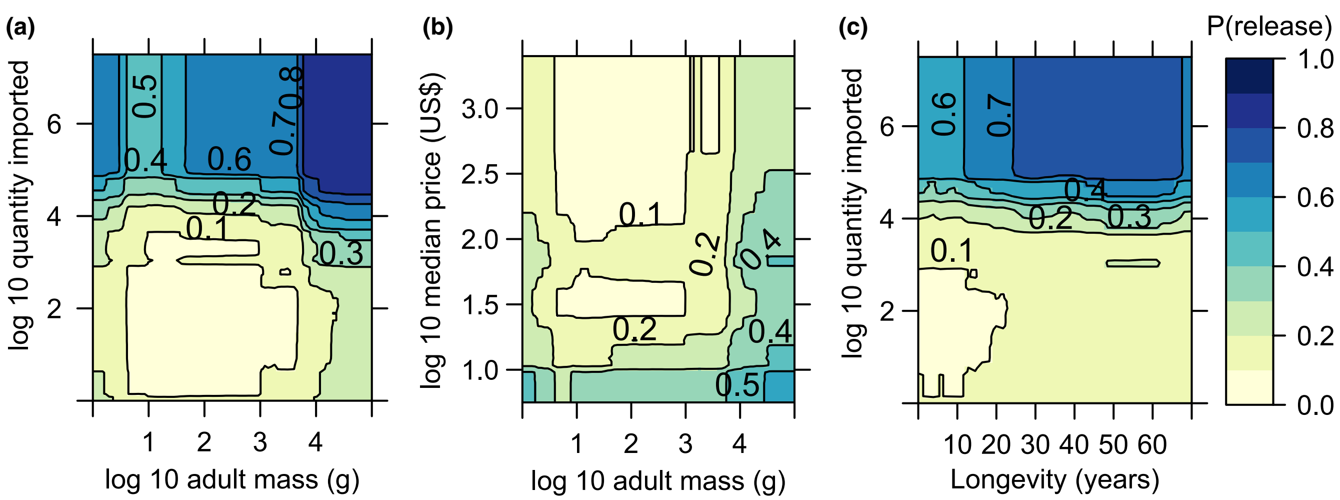

FIGURE 4 Interactions in our boosted regression tree (BRT) model explaining release probability of exotic pet reptiles and amphibians in the US, including (a) quantity imported and adult mass, (b) price and adult mass and (c) quantity imported and longevity. Contour lines with associated numbers represent factor of 10% increases in release probability. Darker shades indicate higher probability of release as predicted from the BRT model. Interaction sizes for each interaction are 56 (a), 16 (b) and 4 (c)

lowest release probability, while larger massed species had higher release probability compared to smaller massed ones (Figure 3). In terms of variable interactions, the strongest was between adult mass and quantity imported (interaction size of 56), where large-bodied species imported in high quantities have three times higher release probability compared to large-bodied species imported in lower quantities (Figure 4a). There was a less strong but similar relationship between quantity imported and longevity whereby long-lived species imported in large quantity have higher release probability compared to long-lived species imported at low quantities (Figure 4c). Finally, we show that adult mass and price interact so that low price and large relative adult mass combine to produce a substantial rise in probability of release (Figure 4b).

4 | DISCUSSION

The pet trade has taken on increased importance in conservation with regard to invasive species (Smith et al., 2009), as is evident from the widespread ecological and economic damage that once-pet species like Burmese python (*Python bivittatus*) and Pacific lionfish (*Pterois volitans*) can produce (Dorcas et al., 2012; Whitfield, Gardner, Vives, & Hare, 2002). Here, we set out to examine the role of biological and economic factors in explaining the first step in the reptile and amphibian invasion pathway, release probability. Our results indicate that there are clear biological and economic factors that increase the probability that exotic pet reptiles and amphibians will be observed as free-living (but not necessarily established) in the conterminous US. These factors reflect the cost of pet care that owners bear over the span of the pet's life and the value that these owners place on the pet's themselves. Notably, we demonstrate that considering both life-history traits and economic characteristics is necessary to determine release probability as the two factors often interact to elevate release probability. This knowledge allows for the proactive development of policy and education tools that can serve to decrease either the prevalence of likely released exotic pets in the market and in homes or encourage owners to responsibly dispose of unwanted pets.

The set of species we record as released are the product of a complex set of individual owner decisions. Our approach seeks to identify broadscale and easily measured factors that effectively capture and describe these decisions. In the absence of extensive pet owner surveys, our approach serves as a reasonable first step to elucidating mechanisms that drive exotic pet releases. We found that reptiles and amphibians that are more abundant on the pet market and are sold at cheaper prices are more likely to be released. This result is consistent with previous research on releases that concludes that pet abundance is a major factor for explaining releases in other exotic pet groups (Duggan et al., 2006; García-Díaz, Ross, Ayres, & Cassey, 2015). Our finding that large adult mass increases release probability is also consistent with previous research for other taxonomic groups (Holmberg et al., 2015; Tingley et al., 2010). Therefore, it is likely that larger species may be a particular cause for concern for releases among most exotic vertebrate pet taxa (birds might be an exception: Su, Cassey, Vall-llosera, & Blackburn, 2015). Furthermore, we show that adult mass and longevity interact with economic factors to either diminish or augment release probability. For instance, long-lived species that are pervasive on the pet market are over three times more likely to be released compared to less commonly sold species of comparable longevity. Similarly, species that achieve a high adult mass while also being common in the market and low-priced are much more likely to be released than species of similar mass that are rare on the market or expensive. One caveat of machine learning methods is that they do not allow explicit testing for phylogenetic signal, which is a shortcoming to our results. Phylogeny was found to be important in a separate study on alien reptiles and amphibians (species not unique to the pet trade; Allen et al., 2017), suggesting that the same may be true with release.

Cross-stage differences in the importance of life history and socio-economic factors are a common feature across all biological invasions (Lockwood, 2017) and our results further highlight the importance of compartmentalising each stage of the invasion process when quantifying risk (Blackburn et al., 2011; Leung et al., 2012). For instance, we show that larger-bodied reptiles and amphibians are more likely to be released; however, after release, other research suggests that smaller-bodied species are more likely to establish self-sustaining populations (from global establishments: Allen et al., 2017; Mahoney et al., 2015). Similarly, our results suggest that import quantity strongly increases release probability for reptiles and amphibians but Fujisaki et al. (2010; Florida only) indicate this same variable does not translate into higher probability of successful establishment in these same taxa. Similarly, there is no reason to suspect that traits that are known to elevate establishment success or invasive spread, such as habitat breadth or competitive ability (Van Wilgen & Richardson, 2012), will have a strong influence on release probability.

Current management options aimed at reducing exotic pet releases include educating the pet-owning public of the ecological risks of releasing their pets (Reaser & Meyers, 2007), or implementation by local agencies of "buy backs" and "amnesty events" for owners seeking to relinquish their pet (Hardin, 2007). Our results provide an initial evidence base to allow such approaches to target particular species, and their owners, making these efforts more effective and efficient in their mission. Specifically, targeting species that are commonly sold *and* large-bodied or long-lived will have the greatest effect in reducing the number of releases. Warning consumers about the zoonotic risks of exotic pets has been shown to decrease the probability when a pet is purchased (Moorhouse, Balaskas, D'Cruze, & Macdonald, 2017). We therefore suggest that a similar strategy of making resources and information available about how a pet's adult size and longevity increases care requirements could help steer consumers away from purchasing reptiles and amphibians they are likely to release after initial purchase (Seekamp, Mayer, Charlebois, & Hitzroth, 2016). In addition, to further help prevent consumers from releasing their exotic pets, it could be beneficial if retailers informed consumers about safe places to surrender their pets such exotic pet shelters, amnesty events or returns/buy backs to the retailers.

Integrating the release stage into risk management can result in a more robust and accurate assessment of invasion risk (e.g., Leung & Mandrak, 2007). Our approach utilizes information common to existing invasion risk assessments (e.g., life-history traits), or can be easily aquired (e.g., current price or popularity), allowing for easier and immediate integration of release risk factors. Such risk assessments have been used to guide legislation aimed at curbing invasions through import bans of high risk species (e.g., through the Lacey Act in the US: Fowler, Lodge, & Hsia, 2007). Our results are particularly helpful in this context as the diversity of reptile and amphibian species sold as pets has been steadily increasing over the last two decades (Romagosa, 2014). Finally, our results can be used to craft legislation targeted at reducing the probability of release of species. For example, our results can be used to target taxing and licensing efforts towards high-release risk species, requiring retailers to only sell single-gendered individuals of a high-release risk species, and "tagging" (via microchips) individuals from high-release risk species. Regardless of the approach, a data-driven effort to document factors that result in exotic pet releases can advance a more comprehensive, evidence-based approach to risk management and policy implementation.

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AUTHORS' CONTRIBUTIONS

O.C.S. and J.L.L. conceived the idea and wrote the manuscript. O.C.S. collected and analysed the data. All authors approved the manuscript.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.j2n732c (Stringham & Lockwood, 2018).

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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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