RESEARCH PAPER

The frog filter: amphibian introduction bias driven by taxonomy, body size and biogeography

Reid Tingley[1]*, Christina M. Romagosa[2], Fred Kraus[3], David Bickford[4], Benjamin L. Phillips[1] and Richard Shine[1]

[1]*School of Biological Sciences A08, University of Sydney, Sydney, NSW 2006, Australia,* [2]*Department of Biological Sciences, 331 Funchess Hall, Auburn University, Auburn, AL 36849-5407, USA,* [3]*Department of Natural Sciences, 1525 Bernice Street, Bishop Museum, Honolulu, HI 96817, USA,* [4]*Department of Biological Sciences, 14 Science Drive 4, National University of Singapore, Singapore 117543, Singapore*

ABSTRACT

Aim Invasive species often exhibit a highly non-random suite of traits relative to non-invasive taxa, and these biases reflect strong selection at a series of steps along the invasion pathway. Here we investigate traits that are favoured in the first of these steps: the introduction of species outside their native geographic range. We use the global introduction of amphibians as our case study.

Location Global.

Methods We examined whether taxonomy, body size and attributes of the native geographic range predict the likelihood of an introduction event in amphibians. We then determined whether these characteristics differed between amphibian species that have been introduced intentionally and those that have been introduced unintentionally (i.e. stowaways).

Results Comparisons of introduced and non-introduced amphibians reveal significant biases with respect to taxonomic position (*c.* 50% of all introduced species originate from only 5% of all families), and characteristics of the native geographic range (most introduced species originate from the Northern Hemisphere, occupy a wide geographic range and are sympatric with high densities of humans). Many of these biases presumably reflect the ease and likelihood of capturing and transporting such animals. Additionally, intentionally introduced species are of larger than average body size, occupy higher elevations in their native ranges, and are more likely to originate from the Northern Hemisphere than unintentionally introduced species.

Main conclusions Introduced amphibian species are not a random subset of the global amphibian fauna with respect to taxonomic affiliation and biogeography, and this restricts our ability to make robust generalizations regarding the ecological determinants of introduction success. Nevertheless, many of our findings are similar to those revealed by previous analyses of vertebrate and invertebrate introductions. Thus, our study suggests that biases in the anthropogenic mechanisms involved in transporting species around the globe are surprisingly consistent across broadly divergent taxa.

Keywords
Alien species, amphibians, Anura, Caudata, introduced species, invasive species, transportation.

Correspondence: Reid Tingley, School of Biological Sciences A08, University of Sydney, Sydney, NSW 2006, Australia. E-mail: reid.tingley@gmail.com

INTRODUCTION

Human activities have introduced species to regions far outside their native geographic ranges. Many introduced species fail, but others thrive and spread widely, inflicting significant damage on native ecosystems (e.g. Ebenhard, 1988; Pimentel, 2002; Kraus, 2009). Given the potential impact of invasive species (and the difficulty of controlling them after they become established) an understanding of why particular taxa become invaders and others do not is critical to the maintenance of biodiversity

(Kolar & Lodge, 2002; Jeschke & Strayer, 2006; Blackburn *et al.*, 2009a). Successful invaders must pass through a series of filters that reflect different stages of the invasion process (Williamson, 1996): transport (which species are moved by humans?); introduction (which species are released into the novel environment?); establishment (which species survive and reproduce?); and spread (which species disperse from the location of introduction?). Importantly, attributes of 'successful' species reflect biases arising through filtering at all of these stages in the sequence: only a non-random subset of all species is likely to pass through each of the four filters (Blackburn & Duncan, 2001; Sol *et al.*, 2008).

Although there is a rich literature on the latter stages of establishment and spread (see Kolar & Lodge, 2001, Hastings *et al.*, 2005, Hayes & Barry, 2008, and Blackburn *et al.*, 2009b, for reviews; see Bomford *et al.*, 2009, for amphibians and reptiles specifically), the initial stages of the invasion pathway have been comparatively understudied (reviewed by Puth & Post, 2005). Studying these initial stages is vital for understanding the determinants of invasion success, because these filters create the array from which all successful invaders are ultimately drawn. Obviously, if a species is never introduced outside its native geographic range, it cannot become an invader (Blackburn & Duncan, 2001). Identifying non-random patterns of introduction allows increased vigilance against high-risk species (Jeschke & Strayer, 2006) and provides information on plausible dispersal routes, pathways and vectors (Carlton & Ruiz, 2005; Blackburn & Cassey, 2007). Prevention is, again, the best medicine.

Most previous analyses of vertebrate introductions have focused on birds (Blackburn & Duncan, 2001; Cassey *et al.*, 2004; Duncan *et al.*, 2006; Blackburn & Cassey, 2007; Blackburn *et al.*, 2009a). These studies have identified major biases with respect to the taxonomy, geographic origin and life-history traits of introduced species. In this paper, we investigate the generality of these findings by examining correlates of introduction probability for a very different taxonomic group: the world's amphibians. The introduction of amphibian species to novel environments can cause declines and genetic changes in native taxa (Arano *et al.*, 1995; Arntzen & Thorpe, 1999; Pagano *et al.*, 2003; Riley *et al.*, 2003; Phillips & Shine, 2004, 2006; Holsbeek & Jooris, 2010), transmit diseases such as chytridiomycosis (Daszak *et al.*, 2004; Garner *et al.*, 2006; Fisher & Garner, 2007) and levy considerable economic costs on recipient jurisdictions (impacts reviewed by Kraus, 2009).

We investigated the following related questions: (1) are introduced amphibians randomly distributed among orders, families and genera; (2) do body size and ecological attributes of the native geographic range influence whether a species has been introduced; and (3) what factors differentiate amphibians that have been introduced intentionally from those that have been introduced unintentionally?

MATERIALS AND METHODS

Data on introduced amphibians were taken from Kraus (2009), and the Global Amphibian Assessment (GAA; http://

www.iucnredlist.org/intiatives/amphibians). The resultant database contained 179 species that were introduced at least once outside their native geographic ranges. We did not include natural colonization events or introductions for conservation purposes. Although data on species introductions are incomplete for many taxa and regions (see Sol *et al.*, 2008; Rodriguez-Cabal *et al.*, 2009), the congruence between the data contained in Kraus (2009) and the GAA suggests that amphibian introductions have been relatively well documented. We restricted our analyses to the orders Anura and Caudata, because only a single introduction from the order Gymnophiona was recorded; a rather obvious taxonomic bias. We tested the hypotheses that among amphibians, probability of introduction was affected by the following species attributes.

1. *Taxonomic affinities.* To determine whether the 179 introduced species were a random taxonomic subset of the global amphibian fauna, we randomly selected 179 species from the total pool of 6004 species that had geographic range data available from the GAA, and calculated the number of species in each order, family and genus (Lockwood, 1999; Blackburn & Duncan, 2001; Romagosa *et al.*, 2009). This procedure was repeated 99,999 times for each taxonomic level. For each order, family and genus, we calculated a two-tailed *P*-value by dividing the number of permutations in which the number of species selected was greater than, equal to, or less than the observed number of introduced species, by the total number of iterations. Because there is debate over the need to adjust for multiple comparisons (Moran, 2003), we judged statistical significance at $\alpha = 0.01$ and 0.05 (Romagosa *et al.*, 2009). Our nomenclature follows that of the GAA, which is in turn closely based on the Amphibian Species of the World database (http://research.amnh.org/herpetology/amphibia).

2. *Availability for transport.* Among birds, widespread species that are easy to obtain are more likely to be introduced (Blackburn & Duncan, 2001; Cassey *et al.*, 2004; Blackburn & Cassey, 2007). We calculated three variables relating to availability for transport: (i) native geographic range size, (ii) mean human population density within each species' native geographic range, and (iii) mean elevation within each species' native geographic range. Range sizes were calculated using equal-area projections of native-range polygons available from the GAA. Human population density was based on United Nations-adjusted census data from 2000 (http://sedac.ciesin.columbia.edu/gpw), whereas elevation was calculated using data from the GLOBE project (http://www.ngdc.noaa.gov/mgg/topo/gltiles.html). Human population density (originally available at 2.5′ resolution) was bilinearly interpolated to a 30′ resolution to match the resolution of the GLOBE data. Both variables were then averaged within each species' range using the Zonal Statistics function in ArcView 9.2© (ESRI, Redlands, CA, USA). We also explored broad-scale geographic effects on introduction probability by assigning the latitudinal mid-point of each species range to either the Northern or the Southern Hemisphere. To normalize the distribution of predictor values, range size and human population density were log-transformed, whereas elevation was square-root-transformed.

3. *Body size.* We used ordinal body-size data gathered by Sodhi *et al.* (2008) to establish four categories for each amphibian order (for anurans: 0–20 mm, 21–50 mm, 51–100 mm, > 100 mm; for caudates: 0–50 mm, 51–100 mm, 101–150 mm, > 150 mm). Snout–vent length was used for anurans, whereas total length was used for caudates (see Sodhi *et al.*, 2008, for further details). Using separate ordinal categories for each order ensured that body-size measurements were directly comparable between orders in our analyses. Because body-size data were available for only 72% (4323/6004) of the species studied, we refitted all models to the reduced dataset to test for consistency in coefficients and model rankings prior to testing for body-size effects.

The analyses above test for differences between amphibian species that have and have not been introduced to places outside their natural range. We then repeated these analyses to ask another question: do the above characteristics differentiate those species that were intentionally introduced from those that were introduced accidentally? Following Kraus (2007, 2009), intentionally introduced species (*n* = 88) were classified as species that were introduced via the pet trade, or for bio-control, food, bait, research or religious purposes. Unintentionally introduced species (*n* = 46) comprised species that were transported via cargo, aquacultural contaminants or the nursery trade. Although some species that were introduced for research purposes (*n* = 11) may have been accidentally released from laboratories, we classified these species as having been introduced intentionally because they were deliberately collected by researchers. Reassigning these species to the unintentional category had negligible effects on our conclusions. Species are often introduced via multiple pathways: those that were introduced intentionally and unintentionally an equal number of times were removed from this analysis, and others were allocated to whichever category (intentional or unintentional) predominated for that species. Three body-size categories were used in this analysis (for anurans: 0–50 mm, 51–100 mm, > 100 mm; for caudates: 0–100 mm, 101–150 mm, > 150 mm), due to low sample sizes in one of the original four size categories.

We used generalized linear mixed-effects models with a logit link and binomial error distribution to investigate effects of range size, human population density, elevation, hemisphere of origin and body size on both probability of introduction, and probability of intentional introduction. To account for taxonomic autocorrelation, order, family and genus were entered as nested random effects; all other variables were treated as fixed effects (Sodhi *et al.*, 2008; Bomford *et al.*, 2009). We accounted for the effects of taxonomy using random effects instead of independent contrasts because a complete phylogeny is lacking for Amphibia, and because categorical variables were included in the analyses (Sodhi *et al.*, 2008). Genus-level random effects were not included in models of intentional introduction probability due to small sample sizes and a subsequent lack of model convergence. This is unlikely to have influenced our results, since most of the taxonomic variation was at the family level. Akaike's information criterion (AIC) was used to determine the strength of evidence for each model relative to the candidate set

of models (*w*AIC). All statistical analyses were conducted in R 2.8.1 using the lme4 and MuMIn libraries (R© Development Core Team, 2008).

RESULTS

Introduced amphibian species were not a random taxonomic subset of the global amphibian fauna at the order, family or genus level (Table 1; see Appendix S1 in Supporting Information). Among the two amphibian orders, anuran species were introduced less frequently than expected (*P* = 0.0003) whereas caudate species were introduced more frequently than expected (*P* = 0.00001). At α = 0.05, 10 families were significantly over-represented in the data; however, when a more stringent α of 0.01 was applied, only eight families were introduced more often than expected. Twenty-seven genera contained significantly more introduced species than would be expected by chance (α = 0.05); most of these were from the 10 over-represented families listed in Table 1 (see Appendix S1). At α = 0.01, 15 genera were over-represented among introduced amphibian species. Genera that were not significantly over-represented at α = 0.01 typically contained one or two introduced species; clearly we cannot make confident statements regarding the introduction potential of these taxa.

Seven families were introduced less frequently than expected at α = 0.05, and three of these remained significantly under-represented at α = 0.01 (Table 1). At α = 0.05, three genera contained significantly fewer species than expected, whereas only one genus was introduced less often than expected at α = 0.01 (see Appendix S1).

Introduced amphibians also were not randomly distributed with respect to their geographical sites of origin (Fig. 1a). The frequency distribution of latitudinal origins of introduced species was strongly left-skewed (skewness = −0.77), with Northern Hemisphere species introduced more often than expected based on latitudinal patterns of amphibian richness (Fig. 1b). Assigning the mid-point of each species' geographic range to the terrestrial ecoregions delimited by Olson *et al.* (2001) revealed additional biases between temperate and tropical regions; over 14% of all temperate species have been introduced, compared with only 1.3% of all tropical species.

Probability of introduction was further affected by factors that facilitate collection and transport (Table 2). A model containing terms for range size, hemisphere of origin, elevation and human population density had relatively high support (*w*AIC = 0.66). The same model without elevation was also moderately supported (*w*AIC = 0.33). Introduction probability decreased with elevation, increased with range size and human population density, and was higher for species originating from the Northern Hemisphere (Figs 1 & 2). With the exception of elevation, the model-averaged 95% confidence intervals of all coefficients did not overlap zero (Table 3). Elevation was a significant predictor of introduction probability in a univariate model, but was negatively correlated with range size (Spearman's ρ = −0.33), suggesting an indirect effect of this variable on introduction probability. Range size was the best predictor of introduction

Table 1 Amphibian families that have been introduced (a) more or (b) less frequently than expected under the null hypothesis of no taxonomic bias.

Order	Family	Observed introduced	Expected introduced	P
(a) Introduced more than expected				
Anura	Alytidae	3	0.33	0.0046
Anura	Bombinatoridae	3	0.29	0.0033
Anura	Hylidae	37	24	0.0057
Anura	Limnodynastidae	5	1.3	0.010
Anura	Pipidae	5	0.90	0.0023
Anura	Ranidae	31	9.2	< 0.0001
Caudata	Ambystomatidae	4	1.0	0.020
Caudata	Cryptobranchidae	3	0.087	< 0.0001
Caudata	Proteidae	2	0.17	0.014
Caudata	Salamandridae	15	2.2	< 0.0001
(b) Introduced less than expected				
Anura	Arthroleptidae	0	3.9	0.020
Anura	Centrolenidae	0	4.3	0.012
Anura	Hyperoliidae	0	5.8	0.0026
Anura	Mantellidae	0	4.9	0.0070
Anura	Megophryidae	1	4.0	0.019
Anura	Strabomantidae	0	15	< 0.0001

Observed and expected columns refer to numbers of species introduced or expected to be introduced.
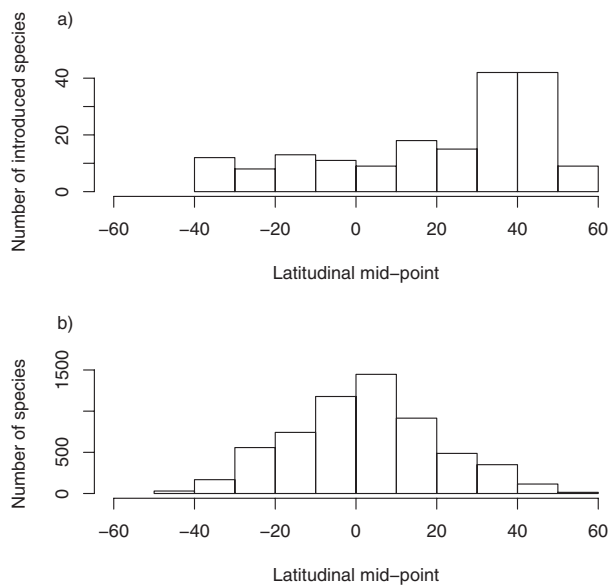
Figure 1 Histograms of latitudinal mid-points for (a) our sample of 179 introduced amphibian species and (b) all 6004 amphibians considered in the analyses.

Table 2 Highest ranked generalized linear mixed-effects models investigating correlates of probability of amphibian introduction.

Model	k	ΔAIC	wAIC
(a) Without body size ($n = 6004$)			
HEM + RANGE + HUMAN + ELEV	8	0	0.66
HEM + RANGE + HUMAN	7	1.4	0.33
(b) Without body size ($n = 4323$)			
HEM + RANGE + HUMAN	7	0	0.61
HEM + RANGE + HUMAN + ELEV	8	0.95	0.38
(c) With body size ($n = 4323$)			
HEM + RANGE + HUMAN + SIZE	10	0	0.55
HEM + RANGE + HUMAN + ELEV + SIZE	11	0.52	0.42

The table shows the number of parameters (k), the difference in Akaike's information criterion (AIC) between each model and the highest ranked model (ΔAIC), and the model weights (wAIC) for the top models comprising > 95% of wAIC. The same models were fitted to: (a) data for 6004 species and (b) data for a subset of 4323 species for which we had body size data. All models were then refitted with body size included as an additional predictor (c). Variables shown are: HEM, hemisphere of origin; RANGE, native geographic range size; HUMAN, human population density within each species' native range; ELEV, elevation within each species' native range; SIZE, body size.

probability in univariate comparisons, followed by elevation (ΔAIC relative to range size model = 230), human population density (ΔAIC = 248) and hemisphere of origin (ΔAIC = 264).

Refitting models with the reduced dataset of 4323 species for which we had data on body size increased model selection uncertainty, again due to the ambiguous contribution of elevation (Table 2). Body size had a significant positive effect in a

univariate comparison, but this effect disappeared after accounting for the four spatial variables. This result was probably due to a positive correlation between body size and range size (Spearman's ρ = 0.24). Indeed, in a univariate model body size was far less able to predict introduction probability than was range size (ΔAIC = 179), and the model-averaged 95% confidence intervals for body size included zero (Table 3).
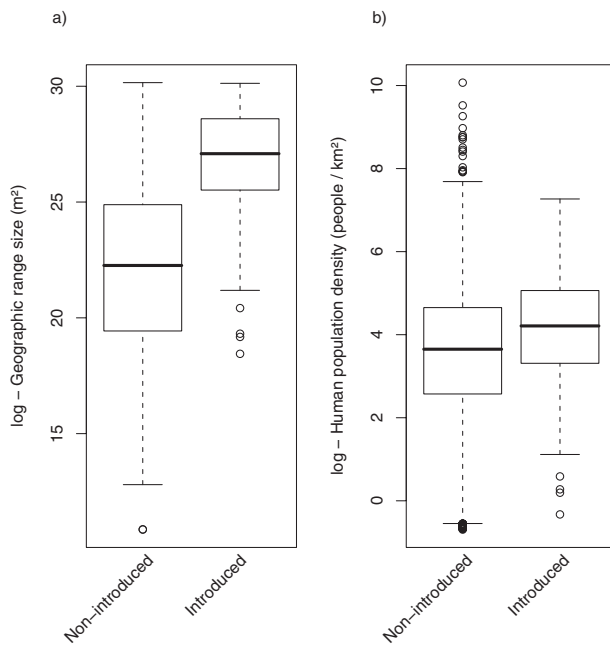
a)   b)

Figure 2 Native geographic range size, and human population density within the native geographic ranges of non-introduced and introduced amphibian species. Boxes represent medians and quartiles, whiskers extend to the most extreme observations that are no more than 1.5 times the interquartile range from the box, and observations which lie outside of this range are shown as points.

Table 3 Results of generalized linear mixed-effects models investigating correlates of amphibian introduction probability.

Variable	Coefficient	Unconditional SE	Lower CI	Upper CI
(a) Without body size ($n = 6004$)				
HEM	1.0	0.33	0.37	1.7
RANGE	0.66	0.054	0.55	0.76
HUMAN	0.49	0.089	0.31	0.66
ELEV	−0.013	0.013	−0.039	0.013
(b) With body size ($n = 4323$)				
HEM	1.0	0.34	0.34	1.7
RANGE	0.61	0.057	0.50	0.72
HUMAN	0.49	0.094	0.30	0.67
ELEV	−0.0063	0.010	−0.026	0.013
SIZE: 2	−0.21	0.89	−2.0	1.5
SIZE: 3	0.40	0.89	−1.4	2.2
SIZE: 4	1.1	0.91	−0.65	2.9

The table shows model-averaged coefficients and their unconditional standard errors and 95% confidence intervals. Models were fitted both with (b) and without (a) body size included as a predictor. See Table 2 for variable abbreviations.

Similar (albeit more uncertain) biases were apparent when we compared amphibian species differing in the reasons for their introduction (intentional versus unintentional). Compared with unintentionally introduced amphibians, intentionally

Table 4 Results of generalized linear mixed-effects models comparing the characteristics of intentionally and unintentionally introduced amphibians.

Variable	Coefficient	Unconditional SE	Lower CI	Upper CI
HEM	1.2	0.73	−0.29	2.6
SIZE: 2	0.45	0.57	−0.66	1.6
SIZE: 3	1.0	0.97	−0.87	2.9
RANGE	−0.058	0.094	−0.24	0.13
HUMAN	−0.027	0.081	−0.19	0.13
ELEV	0.065	0.050	−0.033	0.16

The table shows model-averaged coefficients and their unconditional standard errors and 95% confidence intervals. See Table 2 for variable abbreviations.

introduced amphibians were sympatric with lower densities of humans (Akaike importance weight = 0.22), had smaller geographic ranges (Akaike importance weight = 0.40), were of larger than average body size (Akaike importance weight = 0.64), occupied higher elevations in their native ranges (Akaike importance weight = 0.79) and were more likely to have originated from the Northern Hemisphere (Akaike importance weight = 0.85). However, the model-averaged 95% confidence intervals for all five variables overlapped zero, suggesting a lack of precision in our estimates of these effects (Table 4; see Appendix S2 in Supporting Information).

DISCUSSION

Our results demonstrate strong taxonomic bias in the composition of introduced amphibian species. Nearly 50% of all introduced amphibian species belong to the families Hylidae, Ranidae and Salamandridae, which comprise only 5% of all anuran and caudate families (although they include 21% of all species considered in our analyses). This result echoes strong taxonomic bias found in earlier studies of vertebrate and invertebrate introductions (Lockwood, 1999; Blackburn & Duncan, 2001; Duncan *et al.*, 2006; Ward *et al.*, 2006; Blackburn & Cassey, 2007; Romagosa *et al.*, 2009; cf. Cassey *et al.*, 2004; Suarez *et al.*, 2005).

Six of the 10 families that are over-represented among introduced amphibian species are exclusively found in the Northern Hemisphere, suggesting that taxonomic biases in amphibian introductions may be driven by non-random patterns in the origins of introduced species. Indeed, hemisphere of origin was retained in the highest-ranked model of introduction probability. Previous studies have also found non-random patterns in the origins of introduced ants (Ward *et al.*, 2006; cf. Suarez *et al.*, 2005), plants (Gravuer *et al.*, 2008), fish (Jeschke & Strayer, 2006) and birds (Blackburn & Duncan, 2001; Cassey *et al.*, 2004; Duncan *et al.*, 2006; Blackburn & Cassey, 2007). Geographic biases in the origins of introduced amphibians were likely to be due to high levels of historical and modern trade originating from North America and Europe (Jeschke & Strayer, 2006;

Kraus, 2009). Crosby (1986) has shown that Western imperial expansion from 900–1900 involved wholesale importation of familiar biota to newly colonized territories. The fact that intentionally introduced amphibians were more likely to have originated from the Northern Hemisphere than were stow aways suggests that patterns of amphibian introductions are consonant with Crosby's (1986) findings. However, caudates, which are almost exclusively of Northern Hemisphere origin, have been introduced primarily within the last century, and have been released intentionally in 90% (28/31) of all cases. The tendency for humans to intentionally introduce caudates may therefore also account for Northern Hemisphere biases among intentionally introduced amphibians.

Native geographic range size was the most important predictor of introduction probability, with widespread species having a higher probability of being introduced than species with restricted ranges. This pattern is not an artefact of range-size differences between the Northern and Southern Hemispheres – amphibians centred in the Southern Hemisphere average larger ranges than those centred in the Northern Hemisphere. Instead, the importance of range size was presumably due to the fact that species with large ranges typically have large population sizes (Gaston *et al.*, 2000) and are more likely to be encountered by humans. Range size appears to be the most general predictor of introduction probability across different taxa (Blackburn & Duncan, 2001; Cassey *et al.*, 2004; Jeschke & Strayer, 2006; Blackburn & Cassey, 2007; Gravauer *et al.*, 2008).

High human population density in the native range also was associated with a higher probability of being introduced. García-Berthou *et al.* (2005) found a positive relationship between the number of aquatic species introduced to Europe and human population density within the country of origin. Jeschke & Strayer (2006) found that 'human affiliation' was a significant predictor of which mammals, birds and fish have been introduced to North America and Europe. Collectively, these results suggest that anthropogenic variables should be more routinely included in studies of alien introductions.

Contrary to the results of previous studies, we found only moderate support for an overall effect of body size on introduction probability (Blackburn & Duncan, 2001; Cassey *et al.*, 2004; Jeschke & Strayer, 2006; Blackburn & Cassey, 2007). However, the importance of body size appears to have varied with transportation pathway: large species were more likely to have been transported intentionally, whereas small species were more likely to have been transported by accidental means. Large body size is a desirable trait for species that have been introduced for food or bio-control because large species provide more meat and consume more biomass than small species. Conversely, for unintentionally introduced species, small body size facilitates transport in cargo and nursery materials and decreases the likelihood of pre-export detection.

The fact that humans have intentionally introduced large amphibians illustrates how biases in the early stages of the invasion pathway can ultimately influence invasion success. Intentionally introduced species are often released in larger numbers and afforded greater care in captivity than unintentionally intro-duced species, increasing the likelihood of successful establishment in alien environments (Kraus, 2009). Furthermore, large amphibians generally have broader diets, higher fecundities, greater physiological resistance to desiccation and higher mobility than small species (Duellman & Trueb, 1994). These traits have a direct influence on population growth rates and dispersal, and are thus likely to be important determinants of invasion success. Indeed, many of these traits are possessed by notorious amphibian invaders such as the cane toad *Rhinella marina* (formerly *Bufo marinus* [Linnaeus, 1758]), and the American bullfrog *Lithobates catesbeianus* (formerly *Rana catesbeiana* [Shaw, 1802]). These results demonstrate that we will need to consider all stages of the invasion pathway if we are to make broad generalizations regarding the determinants of invasion success.

CONCLUSION

Introduced amphibian species are a non-random subset of the global amphibian fauna with respect to taxonomic affiliation, geographic origin and attributes of the native geographic range. Most of these biases are readily explicable by intuition, and are consistent with similar biases identified in birds, mammals, fish, plants and ants. Together, these results suggest that the processes of transportation and introduction may generate similar biases in invasive species across broad taxonomic groups. These biases have important implications for our understanding of the final phases of successful invasion: establishment and spread. Additionally, identifying these biases helps focus quarantine efforts to prevent accidental introductions, a growing source of invasive species world-wide.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of amphibian genera that have been introduced more, or less, frequently than expected under the null hypothesis of no taxonomic bias.

Appendix S2 Highest ranked generalized linear mixed-effects models investigating correlates of probability of intentional amphibian introduction.

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BIOSKETCH

Reid Tingley is interested in how small-scale phenomena translate into broad geographic patterns. Much of his research focuses on the ecology and conservation of frogs and turtles.

Editor: Tim Blackburn