LETTER

The influence of traditional Buddhist wildlife release on biological invasions

Xuan Liu[1], Monica E. McGarrity[2], & Yiming Li[1]

[1] Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road, Chaoyang, Beijing 100101, China
[2] Department of Wildlife Ecology and Conservation, University of Florida/IFAS, 110 Newins-Ziegler Hall, PO Box 110430, Gainesville, FL 32611, USA

Keywords
Religion; wildlife release; biological invasions; *Lithobates catesbianus*; establishment; prevention.

Correspondence
Yiming Li, Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road, Chaoyang, Beijing 100101, China.
Tel: +86-10-64807136; fax: +86-10-64807099.
E-mail: liym@ioz.ac.cn

Received
12 September 2011
Accepted
14 December 2011

Editor
Dr. Kendra McSweeney

doi: 10.1111/j.1755-263X.2011.00215.x

Abstract

An understanding of anthropogenic factors influencing wildlife invasions is crucial to development of comprehensive prevention and management strategies. However, little attention has been paid to the role religious practice plays in biological invasions. The tradition of wildlife release is prevalent in many areas around the world where Asian religions are influential and is hypothesized to promote species invasions, although quantitative evidence is lacking. We used an information-theoretic approach to evaluate the influence of Buddhist wildlife release events on establishment of feral populations of American bullfrogs (*Lithobates catesbeianus*) in Yunnan province, southwestern China, from 2008 to 2009. We identified frequency of release events and lentic water conditions as factors that promote establishment of bullfrog populations, whereas hunting activity likely helps to prevent establishment. Our study provides the first quantitative evidence that religious release is an important pathway for wildlife invasions and has implications for prevention and management on a global scale.

Introduction

Invasive species are a growing threat to global biodiversity and there is an urgent need for effective strategies to cope with this ecological issue (Ricciardi 2007). Biological invasions are a complex, multiphase process including initial introduction, establishment of a reproducing population, and dispersal into the recipient habitat (Williamson 2006). An understanding of factors promoting success early in the establishment phase is important for prevention of and rapid response to new invasions (Wilson *et al*. 2009).

Factors affiliated with human activities have been emphasized as key determinants of establishment success among nonindigenous species (Gravuer *et al*. 2008). Release of wildlife for religious purposes is prevalent in many Asian countries, especially those with substantial Buddhist influence (Severinghaus & Chi 1999), but is also well documented in Australia, Canada, and the United States (Table 1) and could contribute to wildlife invasions on a global scale. Reports of religious releases in scientific literature and the popular media span nearly two decades, and indicate that numerous taxa have been released, predominantly by Buddhists and Taoists (Table 1).

Although the influence of religious releases on species invasions has been discussed (Agoramoorthy & Hsu 2005), to our knowledge, there has been no quantitative evaluation of the role of religious release in establishment of introduced species. In response to this paucity of data, we used the American bullfrog (*Lithobates catesbeianus*) as a model species and evaluated the influence of organized, Buddhist release events on establishment of breeding populations of bullfrogs in Yunnan Province, China. The bullfrog is native to eastern North America but has been introduced in many countries and is listed among the "100 of the World's Worst Alien Invasive Species" by the International Union for Conservation of Nature.

Table 1 Evidence for global occurrence of religious wildlife release: Results of a search of literature and news reports

		Taxa released[b]							Religion[c]				
Source[a]	Location	I	F	A	R	B	M	U	B	T	C	P	O/U
Sherwood (2001)	Australia	●	●			●	●		●				
Rutledge (2005)	Australia	●							●				
Severinghaus & Chi (1999)	Cambodia					●							●
Shiu & Stokes (2008)	Canada (Vancouver)							●	●				
Shiu & Stokes (2008)	Canada (Toronto)							●	●				
Shi *et al*. (2009)	China (Mainland)				●				●				
Shiu & Stokes (2008)	China (Tibet)							●	●				
Anonymous (2007)	Hong Kong					●			●				
Chan (2006)	Hong Kong					●			●	●			
Severinghaus & Chi (1999)	Hong Kong					●							●
Severinghaus & Chi (1999)	Malaysia					●							●
Lim & Lim (1992)	Singapore				●								●
Agoramoorthy & Hsu (2005)	Taiwan	●	●	●	●	●	●		●	●			
Agoramoorthy & Hsu (2007)	Taiwan	●	●	●	●	●	●		●	●			
Chen & Lue (1998)	Taiwan				●				●				
Liao *et al*. (2010)	Taiwan		●										
Ling (1972)	Taiwan				●				●				
Severinghaus & Chi (1999)	Taiwan		●		●	●			●	●	●	●	●
I-chia (2011)	Taiwan		●			●			●				●
Kastner (2011)	Taiwan		●		●	●			●	●			●
Harvey (2007)	Thailand					●			●				
Severinghaus & Chi (1999)	Thailand					●							●
Anonymous (1993)	USA (California)				●				●				
Zimmerman & Herrmann (1996)	USA (Illinois)				●								●
Anonymous (2004)	USA (Maryland)		●										●
Guilfoil (2011)	USA (Massachusetts)	●											
West (1997)	USA (New Jersey)		●						●				
Fuoco (2001)	USA (Pennsylvania)	●							●				
Severinghaus & Chi (1999)	Vietnam				●								●
Anonymous (2003)	Vietnam				●				●				

[a]Bibliographic results of a search of literature and news reports, see Appendix S4.
[b]Taxa released: I = invertebrates; F = fish; A = amphibians; R = reptiles; B = birds; M = mammals; U = unspecified.
[c]Religions: B = Buddhism; T = Taoism; C = Catholicism; P = Protestantism; O/U = other/unspecified.

Large release events organized by Buddhist temples are commonplace and temple organizers keep records of these events. According to the Buddhist doctrine of equality of all beings, temples do not designate species for release; rather, they purchase for release all live species available in local markets (Chen 2005). Aquaculture has made bullfrogs widely available in live markets across China (Liu & Li 2009), thus, bullfrogs are likely to be selected for most release events. In addition to their widespread market availability, bullfrogs are also large bodied, frequently highly vocal, and easily identifiable, making this an ideal model species for our study.

Methods

During the bullfrog breeding season (i.e., late April to July) of 2008 and 2009, we conducted intensive surveys in Yunnan province (Figure 1), an area of nearly 400,000 km^{-1} that encompasses a wide range of geographic, economic, and social conditions and diverse religious practices representative of China (Yang *et al*. 1991; Zhao 2001). Yunnan is also situated at the convergence of the Indo-Burma (Myanmar) and South-Central China biodiversity hotspots, a region of global conservation priority (Myers *et al*. 2000).

Temple interviews

In each region ($n = 28$), we visited all Buddhist temples ($n = 95$, regional mean ± SD = 3.4 ± 2.4; range = 2–12) listed by the administrative department of religious affairs and interviewed the designated release event organizer at each temple using a questionnaire (Appendix S1) designed to minimize known biases of interview surveys

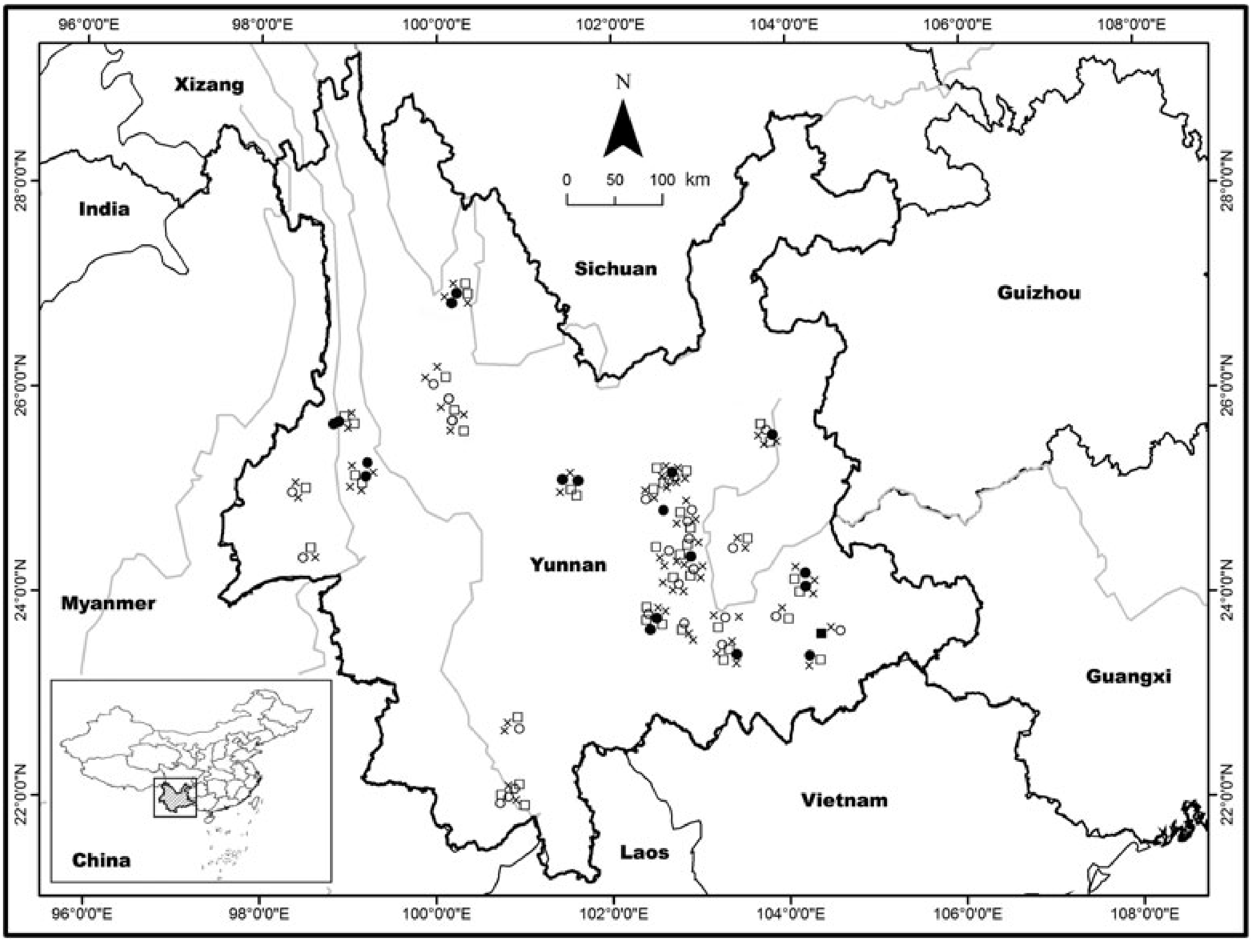

Figure 1 Distribution of surveyed temples ($n = 95$) and of documented breeding populations of bullfrogs among surveyed water bodies ($n = 90$) in our study area. Circles represent water bodies where release events were documented and squares represent control water bodies; filled symbols indicate detection of bullfrog breeding populations. Crosses (X) indicate sampled temples. Some points are superimposed.

in ecological and conservation research (White *et al*. 2005). This designated individual is solely responsible for raising funds, purchasing animals for release, and record keeping for events sponsored by the temple. We showed bullfrog photos to organizers to promote accurate identification and asked them whether bullfrogs were released in events organized by their temple. Recent research has shown that the general public often cannot recognize invasive species without prior education (Somaweera *et al*. 2010). However, this was not a concern in our study because we were in essence asking organizers to identify whether or not they have purchased a familiar, widely available food species, and no similar species of frogs are commonly sold in live markets. If a release event organizer reported purchasing bullfrogs, we asked them to identify local water bodies that served as release sites.

Because propagule pressure influences establishment of invasive species (Lockwood *et al*. 2009), we sought to quantify bullfrog propagule pressure resulting from religious release events. Temple organizers did not record the number of bullfrogs released per event or per year, but reported that the frequency of sponsored release activities at each water body remains constant from year to year because events coincide with sacred days. Temple organizers (12.5%) that did not recall the exact date when they began to release bullfrogs indicated that they began to release bullfrogs as soon as they became available in local markets; we were able to obtain data on timing of bullfrog availability from regional aquatic culture departments. We calculated the cumulative number of bullfrog release events per water body as a proxy for propagule pressure among water bodies; some water bodies served as release sites for multiple temples. Previous studies have recommended this method of estimating propagule pressure by proxy (Lockwood *et al*. 2009; Tingley *et al*. 2011).

Water body surveys

We surveyed 45 water bodies identified by temple organizers as release sites used for organized events and surveyed another 45 randomly selected control water bodies that had no reports of release activity. Because bullfrogs frequently escape from bullfrog farms and invade water bodies within 1 km (Liu & Li 2009), which could easily confound results, we consulted regional aquatic culture departments and surveyed local farmers to identify the location of farms currently or historically used to raise bullfrogs and excluded water bodies with a history of bullfrog farming within a 1-km radius. Because genetic evidence indicates that bullfrog migration may also occur over long distances (Austin *et al*. 2004), we also included distance to the nearest bullfrog farm as a factor in our analysis. After selecting control water bodies, we revisited temples to confirm that these water bodies had never been used for religious release events. We were able to survey every active temple in each region except for in Kunming, where we surveyed 10 of 12 temples.

We used a handheld GPS (Magellan eXplorist210, Santa Clara, CA, USA) to record the location of each water body and mapped the location using ArcGIS Version 9.1 (ESRI, Redlands, CA, USA). We estimated maximum water depth of each water body and quantified percent vegetative coverage based on surveys of a 1-m wide swath of shoreline adjacent to frog survey transects (Li *et al*. 2006). We described shading as the average of four clinometer measurements (i.e., in each cardinal direction) of the angle from the center of each water body to the top of the tree line or horizon (Pearl *et al*. 2005). We categorized water bodies dichotomously as permanent-lentic (i.e., conditions favorable for bullfrogs) or other, based upon direct observations. Previous studies of bullfrog physiological requirements indicate that permanent, lentic waters are a key requirement for bullfrogs (Li *et al*. 2006; Maret *et al.* 2006; Liu & Li 2009).

We used visual encounter surveys along shoreline transects (Jaeger 1994) at each water body to investigate the presence of bullfrog breeding populations and evaluate species richness of native frogs. We divided the accessible shoreline of each water body into 2–5 segments (<100 m/segment) based on the shoreline length after excluding inaccessible areas (Li *et al*. 2006), and randomly located a line transect within each segment. Transects (2 m × 10 m) followed the shoreline with half the width (i.e., 1 m) in the water and half on the shore. Two observers simultaneously searched line transects for bullfrogs at night (19:00–22:00) with the aid of an electric torch (12-V DC lamp, Qingtianzhu 201, Northwestern light Industry Company, Xi'an, China) for three consecutive nights (Jaeger 1994). We also used a 0.5-cm dip net to sample the water along the shoreline to evaluate evidence of successful bullfrog breeding, such as the presence of eggs, tadpoles, or subadults (Jaeger 1994); we made 50, 2-m sweeps with the dip net per transect. Because only adults were available in the market and only adults were released by temples, the presence of eggs, tadpoles, or subadults is unequivocal evidence of reproduction in the wild. We identified native frog species by appearance and/or vocalizations with the help of a guidebook (Fei 1999), and collected specimens to confirm identifications when necessary. We also recorded any observations of humans hunting bullfrogs to validate and augment farmer reports of hunting activity.

Farmer interviews

We randomly selected two local farmers near surveyed water bodies ($n = 90$) during field surveys and interviewed them using a standardized questionnaire (Appendix S2). Farmers are generally well informed about organized release events, which are special occasions; therefore, we used farmer interviews to verify temple organizer reports of release events (accordance rate = 98.6%) and confirm absence of organized release activities at control water bodies. We also used farmer interviews to classify the degree of bullfrog hunting pressure at each surveyed water body dichotomously as frequent (1) or nonexistent to minimal (0). Responses for each site were highly consistent between farmers, and were also highly consistent with our own direct observations (accordance rate = 99.3%). We also asked farmers to identify the location of current or historical bullfrog farms in the vicinity. Farmer responses were consistent with records from regional aquatic culture departments (accordance rate = 100%).

Additional data

We estimated the area of each water body from satellite images using ArcGIS. We obtained elevation and climate information for each water body from the WorldClim database (http://www.worldclim.org/), including average (1950–2000) temperature of the coldest quarter and warmest quarter and annual precipitation data. We selected climate variables based on bullfrogs' requirements for thermal energy and water availability (Ficetola *et al*. 2007). Previous studies suggest that human-modified landscapes can facilitate bullfrog invasions (Ficetola *et al*. 2007); therefore, we also obtained human footprint index (http://www.ciesin.columbia.edu/wild_areas/) as a factor in our analysis.

Table 2 Characteristics of release and control water bodies surveyed in Yunnan province, China. Values are proportions or means ± 1 SE

	Water body type	
Characteristic	Release	Control
Proportion with bullfrog breeding populations	21/45	1/45
Log_{10} (release frequency)	2.09 ± 0.07	0
Proportion with permanent lentic water conditions[a]	32/45	32/45
Log_{10} (water area; m^2)	4.44 ± 0.17	4.46 ± 0.18
Water depth (m)	3.09 ± 0.40	2.41 ± 0.24
Shading	31.27 ± 1.93	30.73 ± 1.97
Distance to nearest bullfrog farm (km)	2.45 ± 0.09	2.53 ± 0.13
Vegetation cover[b]	3.29 ± 0.22	3.24 ± 0.19
Proportion with frequent hunting	22/45	26/45
Native frog species richness	4.31 ± 0.13	4.33 ± 0.14
Altitude (m)	1640.5 ± 63.89	1620.33 ± 65.48
T_s (°C)	22.09 ± 0.32	22.18 ± 0.39
T_w (°C)	11.50 ± 0.42	11.34 ± 0.39
Annual precipitation (mm)	1033.53 ± 21.93	1055.16 ± 25.20
Human footprint index	44.69 ± 2.69	44.64 ± 2.51
Region	28	28

[a]Water condition was included in the model as a dichotomous variable (i.e., permanent-lentic or other type).
[b]Vegetation coverage category of each water body as follows: 1 = 0%, 2 = 1–10%, 3 = 11–20%, etc.

Statistical analysis

Before analysis, we ($\log_{10}(n + 1)$) transformed data for water body area and propagule pressure to improve normality of data distribution. We used a chi-square test to evaluate differences in proportion of water bodies with bullfrog breeding populations between release and control sites. We used multivariate analysis of variance (MANOVA) to compare characteristics (Table 2) between release and control water bodies. We conducted generalized linear mixed models (GLMM) using the lme4 package in R (Version 2.13.1, function lmer, R Development Core Team 2011), with establishment of bullfrog breeding populations as the binary response variable, and included the following thirteen explanatory variables: relative propagule pressure (i.e., total bullfrog release events; range = 0–36), hunting pressure category, human footprint index, distance to nearest bullfrog farm, water area, water depth, water condition (i.e., permanent-lentic or other), vegetation percentage, shading, temperature, precipitation, and native frog species richness. Because there may be considerable regional similarity in prevalence of release activities and distribution of temples and water bodies are nonindependent, we also included region identity as a random effect in our analyses to control for potential spatial pseudoreplication (Bolker *et al*. 2009). Before regression analysis, we found most predictor variables to be free of multicolinearity (i.e., Pearson correlation coefficient, $r \geq 0.85$; Berry & Feldman 1985), except between altitude and temperature (i.e., T_s and T_w). Because altitude influences temperature, we eliminated altitude and retained temperature variables. We, then, used the information-theoretic approach and applied a model averaging procedure to make a more reliable inference from an entire set of models rather than selecting a single best model (Whittingham *et al*. 2006). We also used all possible combinations of the thirteen variables (i.e., $2^{13}-1 = 8{,}191$ models) and compared alternative models using the Akaike's information criterion (AIC_c), corrected for small sample size (Burnham & Anderson 2002; Appendix S3) using the dredge and model averaging functions in package MuMIn in R.

Results

We found evidence of bullfrog breeding (i.e., presence of multiple life stages) in 22 surveyed water bodies in Yunnan Province (Figure 1); bullfrog-breeding populations were present at a significantly greater proportion of release water bodies (21/45) than control water bodies (1/45) where release events had not occurred ($\chi^2 = 24.06$, $P < 0.001$). However, characteristics did not differ significantly between release and control water bodies (i.e., all $P > 0.1$; Table 2).

The multimodel inference based on the information-theoretic approach revealed that release frequency, presence of permanent, lentic water, and hunting activities had the greatest relative importance for the establishment of bullfrog breeding populations (Table 3). Establishment of bullfrog breeding populations was negatively related to the intensity of hunting activities and positively related to the other two variables (Table 3).

Discussion

Our study provides the first quantitative evidence that release of wildlife for religious ceremonial purposes can promote establishment of nonindigenous species. Human-mediated propagule pressure is a key factor influencing species invasions (Lockwood *et al*. 2009). Increased frequency of release events increases propagule pressure and was related to increased likelihood of bullfrog establishment in our study. Human footprint, a composite factor integrating urbanization, population density, transportation networks, and other human activities (Sanderson 2002), has been implicated in bullfrog establishment on a global scale (Ficetola *et al*. 2007), but our

Table 3 Model-averaged parameter estimates of generalized linear mixed model (GLMM) with the presence of bullfrog breeding populations at surveyed water bodies ($n = 90$) in Yunnan province, China as the response variable. Parameters were estimated based on model averaging over all 8,191 models. The relative importance of a predictor variable was calculated by summing the Akaike weights across all of the models for the variable

Explanatory variables	Relative importance	Parameter estimate	Variance
Log_{10} (release frequency)	0.995673	6.23	1.65
Proportion with permanent lentic water conditions[a]	0.834278	2.77	1.27
Log_{10} water area (m^2)	0.193244	−0.0527	0.205
Water depth (m)	0.278109	0.0441	0.118
Shading	0.134540	−0.000552	0.0143
Distance to nearest bullfrog farm (km)	0.124770	0.013	0.237
Vegetation cover category[b]	0.151901	0.0293	0.182
Proportion with frequent hunting	0.991654	−1.63	1.21
Native frog species richness	0.117850	−0.00763	0.17
T_s (°C)	0.164322	0.0211	0.151
T_w (°C)	0.203136	−0.0354	0.133
Annual precipitation (mm)	0.131988	−0.000228	0.00147
Human footprint index	0.160991	0.00272	0.0133

[a]Water condition was included in the model as a dichotomous variable (i.e., permanent-lentic or other type).
[b]Vegetation coverage category of each water body as follows: 1 = 0%, 2 = 1–10%, 3 = 11–20%, etc.

results suggest that human footprint exerts little influence on bullfrog establishment in our study area. However, hunting pressure, a human activity that is not considered in the composite human footprint factor, was negatively related to bullfrog occurrence, suggesting that this human activity may serve to limit bullfrog invasions (Li *et al*. 2006; Ficetola *et al*. 2007).

Our finding that bullfrog breeding populations are significantly more likely to occur at sites with permanent, lentic waters is consistent with previous studies that identified these water conditions as a critical physiological requirement of bullfrogs (Maret *et al*. 2006). Climate variables were not significant in our study, suggesting that suitable conditions for bullfrog invasion existed at all water bodies; this is consistent with predictions based on ecological niche models (Ficetola *et al*. 2007). Although high native species richness often confers a higher resistance to biological invasions (Shea & Chesson 2002), we found no significant effect of native amphibian species richness on establishment of invasive species. This result is consistent with numerous previous studies (Fridley *et al*. 2007); however, other factors, such as predator abundance, could influence establishment (Adams *et al*. 2003) and may warrant investigation.

Bullfrog farms are a well-known source of bullfrog invasions in China, and we previously found that bullfrogs frequently invade water bodies within ≤1 km of these facilities (Liu & Li 2009). We controlled for this by excluding water bodies within 1 km of known farms from our study, and also included distance to nearest known bullfrog farm as a factor in our analysis. The lack of significance of this proximity factor confirms that, although bullfrogs are capable of long distance overland movements (Austin *et al*. 2004), bullfrog presence at our sites was likely the result of religious release rather than farming activity.

Conservation and management recommendations

We found that bullfrogs have invaded numerous water bodies in Yunnan province through the religious release pathway. Bullfrogs are large, generalist predators and disease vectors for chytrid fungus (*Batrachochytrium dendrobatidis*; *Bd*; Garner *et al*. 2006), a major cause of global amphibian decline (Wake & Vredenburg 2008). Invasive bullfrogs could have significant negative impacts on native amphibians in Yunnan through predation (Wu *et al*. 2005) and larval competition (Kupferberg 1997), and may have already been instrumental in causing the extinction of one salamander species (He 1998). Moreover, we previously detected *Bd* in feral bullfrog populations in Yunnan (Bai *et al*. 2010), and caution that invasive bullfrogs pose a significant threat to native amphibians that should not be underestimated.

As a result, it is essential to explore all possible avenues for development of comprehensive prevention plans. Although we cannot support public promotion of bullfrog hunting as a management tool, government-regulated hunting programs could provide professionals with species identification knowledge and offer permits for hunting bullfrogs at water bodies where they are frequently released (Somaweera *et al*. 2010). Moreover, we suggest that prohibition of live sale of certain high-risk species may be warranted, and prohibition of nonindigenous wildlife release and monitoring of aquaculture facilities is critical. Prevention of invasions requires not only enactment and strict enforcement of appropriate laws and regulations but also requires that regulations be widely publicized.

Our findings indicate that religious wildlife release can play an integral role in the establishment of breeding populations of nonindigenous species. Release of animals for religious purposes is ancient practice in several religions of Asian origin, especially Buddhism and Taoism, mainstream religions practiced around the world (Severinghaus & Chi 1999), and is unlikely to be abandoned.

Religious wildlife releases are well documented across Asia, are already considered problematic in Canada and Australia, and are likely much more widespread than is known (Shiu & Stokes 2008). Reports of religious wildlife release from around the world span more than a decade (Table 1), and this invasion pathway is hypothesized to be responsible for several species invasions, including the establishment of Asian swamp eels (*Monopterus albus*) in the United States (Nico *et al*. 2011). The significance of this pathway, both for promoting and preventing invasions, should not be taken lightly. Our study shows that the large number of propagules introduced during organized, religious events is highly conducive to establishment of the introduced species when the introduced habitat provides appropriate conditions. However, Buddhist ethics include deep respect for the environment (Nasr 1996; Shiu & Stokes 2008; Dudley *et al*. 2009; Bhagwat *et al*. 2011) and Buddhists would not likely knowingly release invasive species that are detrimental to the native ecosystem. Our survey results suggest that such releases could be prevented through education, and through promotion of responsible religious release activities (e.g., for conservation purposes). Government or NGOs could sponsor breeding programs for imperiled, native species and coordinate with local temples to hold ceremonial release or reintroductions events at designated water bodies as a means of reducing species introductions and establishment. Our findings are widely applicable and provide a scientific basis for timely efforts to address preventable species invasions on a global scale.

Acknowledgments

We thank C.M. Bai and Y. Luo for field assistance and the "973" program (2007CB411600), China National Science Foundation (30870312), and the Chinese Academy of Sciences (kscx2-yw-z-1021) for financial support. We also thank P. Levin, K. McSweeney, and anonymous reviewers for constructive comments on an earlier draft of this manuscript. This study was approved by the Animal Care and Ethics Committee, Institute of Zoology, Chinese Academy of Sciences.

Supporting Information

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

Appendix S1. Questionnaire used to interview release event organizers at each temple.

Appendix S2. Questionnaire used to interview farmers in the vicinity of each water body to verify temple organizer reports and obtain information on other human activities (i.e., bullfrog hunting and farming). We also recorded sex of each farmer interviewed.

Appendix S3. Model averaging process used to evaluate the relative importance of each variable based on an information-theoretic method.

Appendix S4. Evidence for global occurrence of religious wildlife release: Bibliographic results of a search of literature and news reports, shown in Table 1. (Databases searched: ISI Web of Knowledge, Chinese Journal Full-text Database, Google Scholar, and Google News; Search terms included combinations of the following: "religion," "religious," "release," "free," "fang sheng," "prayer," "ritual," "festival," "Vesak day," "Buddhist," "Buddhism," "Taoism," "ritual," "ceremony," "animal," "wildlife," "fish," "turtle," "frog," and "bird.")

References

Adams, M.J., Pearl, C.A., Bury, R.B. (2003) Indirect facilitation of an anuran invasion by non-native fishes. *Ecol Lett* **6,** 343–351.

Agoramoorthy, G., Hsu, M.J. (2005) Religious freeing of wildlife promotes alien species invasion. *Bioscience* **55,** 5–6.

Austin, J.D., Lougheed, S.C., Boag, P.T. (2004) Controlling for the effects of history and nonequilibrium conditions in gene flow estimates in northern bullfrog (*Rana catesbeiana*) populations. *Genetics* **168,** 1491–1506.

Bai, C.M., Garner, T.W.J., Li, Y.M. (2010) First evidence of *Batrachochytrium dendrobatidis* in China: discovery of Chytridiomycosis in introduced American bullfrogs and native amphibians in the Yunnan province, China. *EcoHealth* **7,** 127–134.

Berry, W., Feldman, S. (1985) *Multiple regression in practice*. Sage, Beverly Hills, CA.

Bhagwat, S.A., Dudley, N., Harrop, S.R. (2011) Religious following in biodiversity hotspots: challenges and opportunities for conservation and development. *Conserv Lett* **4,** 234–240.

Bolker, B.M., Brooks, M.E., Clark, C.J. *et al*. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* **24,** 127–135.

Burnham, K.P., Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach.* Springer Verlag, New York.

Chen, X.Q. (2005) Significance, implementation and notes on Buddhist release of animals. *The Voice of Dharma* **4,** 42–48.

Dudley, N., Higgins-Zogib, L., Mansourian, S. (2009) The links between protected areas, faiths, and sacred natural sites. *Conserv Biol* **23,** 568–577.

Fei, L. (1999) *Atlas of amphibians of China*. Henan Press of Science and Technology, Zhengzhou.

Ficetola, G.F., Thuiller, W., Miaud, C. (2007) Prediction and validation of the potential global distribution of a problematic alien invasive species—the American bullfrog. *Divers Distrib* **13,** 476–485.

Fridley, J.D., Stachowicz, J.J., Naeem, S. *et al*. (2007) The invasion paradox: reconciling pattern and process in species invasions. *Ecology* **88,** 3–17.

Garner, T.W.J., Perkins, M.W., Govindarajulu, P. *et al*. (2006) The emerging amphibian pathogen Batrachochytrium dendrobatidis globally infects introduced populations of the North American bullfrog, *Rana catesbeiana*. *Biol Lett* **2,** 455–459.

Gravuer, K., Sullivan, J.J., Williams, P.A., Duncan, R.P. (2008) Strong human association with plant invasion success for *Trifolium* introductions to New Zealand. *Proc Natl Acad Sci USA* **105,** 6344–6349.

He, X.R. (1998) *Cynops wolterstorffi*, an analysis of the factors caused its extinction. *Sichuan J Zool* **17,** 58–60.

Jaeger, R. (1994). Standard techniques for inventory and monitoring (Transect sampling). Pages 97–102 in W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, M. S. Foster, editors. *Measuring and monitoring biological diversity, standard methods for amphibians.* Smithsonian Institution Press, Washington, D.C.

Kupferberg, S.J. (1997) Bullfrog (*Rana catesbeiana*) invasion of a California river: the role of larval competition. *Ecology* **78,** 1736–1751.

Li, Y.M., Wu, Z.J., Duncan, R.P. (2006) Why islands are easier to invade: human influences on bullfrog invasion in the Zhoushan archipelago and neighboring mainland China. *Oecologia* **148,** 129–136.

Liu, X., Li, Y.M. (2009) Aquaculture enclosures relate to the establishment of feral populations of introduced species. *PLoS One* 4(7): e6199. doi:10.1371/ journal.pone.0006199.

Lockwood, J.L., Cassey, P., Blackburn, T.M. (2009) The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Divers Distrib* **15,** 904–910.

Maret, T.J., Snyder, J.D., Collins, J.P. (2006) Altered drying regime controls distribution of endangered salamanders and introduced predators. *Biol Conserv* **127,** 129–138.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403,** 853–858.

Nasr, S. (1996) *Religion and the order of nature.* Oxford University Press, Oxford.

Nico, L.G., Sharp, P., Collins, T.M. (2011) Imported Asian swamp eels (Synbranchidae: *Monopterus*) in North American live food markets: potential vectors of non-native parasites. *Aquatic Invasions* **6,** 69–76.

Pearl, C.A., Adams, M.J., Leuthold, N., Bury, R.B. (2005) Amphibian occurrence and aquatic invaders in a changing landscape: implications for wetland mitigation in the Willamette Valley, Oregon, USA. *Wetlands* **25,** 76–88.

R Development Core Team. (2011) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ricciardi, A. (2007) Are modern biological invasions an unprecedented form of global change? *Conserv Biol* **21,** 329–336.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G. (2002) The human footprint and the last of the wild. *Bioscience* **52**, 891–904.

Severinghaus, L.L., Chi, L. (1999) Prayer animal release in Taiwan. *Biol Conserv* **89,** 301–304.

Shea, K., Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol Evol* **17,** 170–176.

Shiu, H., Stokes, L. (2008) Buddhist animal release practices: historic, environmental, public health and economic concerns. *Contemporary Buddhism* **9,** 181–196.

Somaweera, R., Somaweera, N., Shine, R. (2010) Frogs under friendly fire: how accurately can the general public recognize invasive species? *Biol Conserv* **143,** 1477–1484.

Tingley, R., Phillips, B.L., Shine, R. (2011) Establishment success of introduced amphibians increases in the presence of congeneric species. *Am Nat* **177,** 382–388.

Wake, D.B., Vredenburg, V.T. (2008) Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proc Natl Acad Sci USA* **105,** 11466–11473.

White, P.C.L., Jennings, N.V., Renwick, A.R., Barker, N.H.L. (2005) Questionnaires in ecology: a review of past use and recommendations for best practice. *J Appl Ecol* **42,** 421–430.

Whittingham, M.J., Stephens, P.A., Bradbury, R.B., Freckleton, R.P. (2006) Why do we still use stepwise modelling in ecology and behaviour? *J Anim Ecol* **75,** 1182–1189.

Williamson, M. (2006) Explaining and predicting the success of invading species at different stages of invasion. *Biol Invasions* **8,** 1561–1568.

Wilson, J.R.U., Dormontt, E.E., Prentis, P.J., Lowe, A.J., Richardson, D.M. (2009) Something in the way you move: dispersal pathways affect invasion success. *Trends Ecol Evol* **24,** 136–144.

Wu, Z.J., Li, Y.M., Wang, Y.P., Adams, M.J. (2005) Diet of introduced Bullfrogs (*Rana catesbeiana*): predation on and diet overlap with native frogs on Daishan Island, China. *J Herpetol* **39,** 668–674.

Yang, D., Li, S., Liu, W., Lu, S. (1991) *Amphibian fauna of Yunnan, China*. Forestry Publishing House, Beijing.

Zhao, B.L. (2001) The multi-ethnic flavor in the Buddhist culture of Yunnan research group of Buddhist culture tourism development. *Yunnan University J Hum Soc Sci* **27,** 89–92.

