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Why islands are easier to invade: human influences on bullfrog invasion in the Zhoushan archipelago and neighboring mainland China

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Abstract Islands are often considered easier to invade than mainland locations because of lower biotic resistance, but this hypothesis is difficult to test. We compared invasion success (the probability of establishing a wild reproducing population) for bullfrogs (*Rana catesbeiana*) introduced to enclosures on 26 farms on islands in the Zhoushan archipelago and 15 farms in neighboring mainland China. Bullfrogs were more likely to invade farms located on islands with lower native frog species richness than mainland farms, consistent with the biotic resistance hypothesis. However, human frog hunting pressure also differed between islands and the mainland and, along with the number of bullfrogs raised in enclosures, was a stronger predictor of invasion success than native frog richness in multiple regression. Variation in hunting pressure was also able to account for the difference in invasion success between islands and mainlands: islands had lower hunting pressure and thus higher invasion probability. We conclude that the ease with which bullfrogs have invaded islands of the Zhoushan archipelago relative to the mainland has little to do with biotic resistance but results from variation in factors under human control.

Keywords Biotic resistance · Island susceptibility · Propagule pressure · Hunting pressure

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Introduction

A classic paradigm in ecology is that islands are easier to invade than mainland locations (Elton 1958; Carlquist 1965; Wilson 1965; MacDonald and Cooper 1995). This idea derives from the empirical observation that island biotas often contain a greater proportion of exotic species than mainland biotas (Elton 1958; Atkinson 1989), and from ecological theory arguing that species-rich (mainland) communities better resist invasion than species-poor (island) communities (Elton 1958; MacArthur 1955, 1970, 1972; Case 1991; but see also Levine and D'Antonio 1999). One mechanism thought to underlie this pattern is that a greater number of species results in greater resource utilization, leaving fewer resources available for an invader to exploit. Because islands are species poor and have a simpler food web structure relative to equivalent mainland locations, this is hypothesized to result in lower "biotic resistance" to potential invaders (Mayr 1965; Elton 1958; Wilson and Bossert 1971; Pimm 1991).

While it appears straightforward, the biotic resistance hypothesis as it relates to islands is difficult to test for two reasons. First, to control for potentially confounding factors we would want to examine the probability of invasion (the successful establishment of a wild reproducing population) of the same species at both island and mainland locations under identical conditions (Simberloff 1995; Case 1996; Sol 2000). This is difficult to achieve because of the logistical and ethical difficulties of conducting a large-scale invasion experiment replicated across island and mainland sites. Nevertheless, for some taxa (notably birds) there exist records of past human-assisted introductions to different locations around the world. Several studies have used these data to test whether introductions to islands are more or less likely to succeed whilst statistically controlling for other factors known to influence invasion outcomes (Sol 2000; Blackburn and Duncan 2001; Cassey 2003). These studies generally reveal no difference between islands and mainlands in the probability of invasion.

Second, even if invasion success is found to be greater on islands, islands frequently differ from mainlands in characteristics other than species diversity that could affect invasion outcomes (D'Antonio and Dudley 1995). Islands, for example, are often characterized as being especially prone to disturbance, which in turn may increase susceptibility to invasion (MacDonald and Cooper 1995). Hence, differences in species diversity (and hence biotic resistance) may be only one of several plausible explanations for differences in island–mainland invasibility.

In this study we compare invasion success following the introduction of bullfrogs (*Rana catesbeiana*) to islands in the Zhoushan archipelago and the neighboring mainland of China in order to test the biotic resistance hypothesis. Our study is unique in that we have replicated introductions of a species to numerous island and mainland locations in the same vicinity, and because we are able to control statistically for other confounding factors known to influence introduction success, notably propagule pressure (Cassey et al. 2004), and thus to determine the relative importance of species diversity versus other factors in explaining differences in island–mainland invasibility. If the biotic resistance hypothesis holds, we predict that: (1) bullfrogs will have a higher probability of invading island than mainland locations, and (2) that differences in invasibility will be best explained by the lower diversity of native frog communities in island relative to mainland locations.

Materials and methods

Study species

The bullfrog is one of the 100 "world's worst" invaders (ISSG 2002), leading to population declines and local extinctions of native amphibians in many parts of the world (Moyle 1973; Bury and Luckenbach 1976; Fisher and Shaffer 1996; Kiesecker and Blaustein 1997; Kupferberg 1997; Kats and Ferrer 2003). Native to the eastern United States and the Great Plains region, with some populations reaching into Nova Scotia, Canada (Moyle 1973; Bury and Whelan 1985), since the end of the nineteenth century bullfrogs have been introduced into California and Hawaii, British Columbia, Mexico, the Caribbean Islands, Brazil, the Far East and Europe. The frog was introduced to Chinese Taiwan in 1924, and mainland China in 1959 (Wu et al. 2004). Since then, captive bullfrog populations have been introduced to most provinces of China. Captive bullfrogs were introduced to Zhoushan archipelago and the neighboring mainland in the mid 1980s with the purpose of raising bullfrogs for sale in local markets, and many small farms began raising bullfrogs within enclosures built in rice fields, pools or reservoirs on the property. Wild populations of bullfrogs in these areas derive from frogs escaping from the enclosures (Wu et al. 2004). Local people often hunt native pond frogs (*Rana nigromaculata*) along with bullfrogs naturalized in the wild.

Study area

The study was carried out in Zhoushan archipelago (29°32′–31°04′N and 121°30′–123°25′E) and adjacent mainland (29°35′–29°59′N and 121°34′–121°57′E), Northeast Zhejiang province, China (Fig. 1). Zhoushan archipelago consists of 1,339 islands in the East China Sea (Zhou 1987), with a total land area of about 1,371 km^2, and with 52 islands >1 km^2. Zhoushan is the largest island with an area of 468.7 km^2. People inhabit 98 of the islands and fishing is the primary occupation. The islands of Zhoushan archipelago were originally part of the neighboring mainland but became separated from the area around Ninbo City and Xiangshan County around 7,000–9,000 years ago due to the sea level rising in the late Pleistocene (Wang and Wang 1980; Zhou 1987). Most of the people in Ninbo City and Xiangshan County are farmers.

Zhoushan archipelago and the adjacent mainland have similar topography, climate, vegetation and faunas (Zhou 1987; Yu 1989; Zhuge 1990; Huang 1990). Both are in the coastal hill–plain zone of Zhejiang province, covered with hills (70% of total area) and plains (30% of total area). The highest peak on the mainland is 657 m elevation compared to 544 m in Zhoushan archipelago. The natural vegetation of the area is dominated by subtropical evergreen broadleaf forest. The climate is typical of the subtropical ocean monsoon zone and is highly seasonal, with hot summers and cool winters. The average annual temperature on the mainland and archipelago is the same (16.3°C), with a range from 5.1°C in January and 27.7°C in July on the mainland, and 5.7°C in January and 26.7°C in July on Zhoushan archipelago. Annual rainfall is about 1,200–1,400 mm. Being land-bridge islands, the faunas of the mainland and archipelago have the same origin, but overall species richness is lower on the islands than the neighboring mainland. There are a total of 17 species of amphibian found on the mainland and ten species on the Zhoushan archipelago (Huang 1990; Yiming et al. 1998).

Study methods

There are possibly >100 farms that used to raise or are still raising bullfrogs in Zhoushan archipelago and the adjacent mainland. Farmers usually raised bullfrogs within enclosures located in one of three habitats: rice

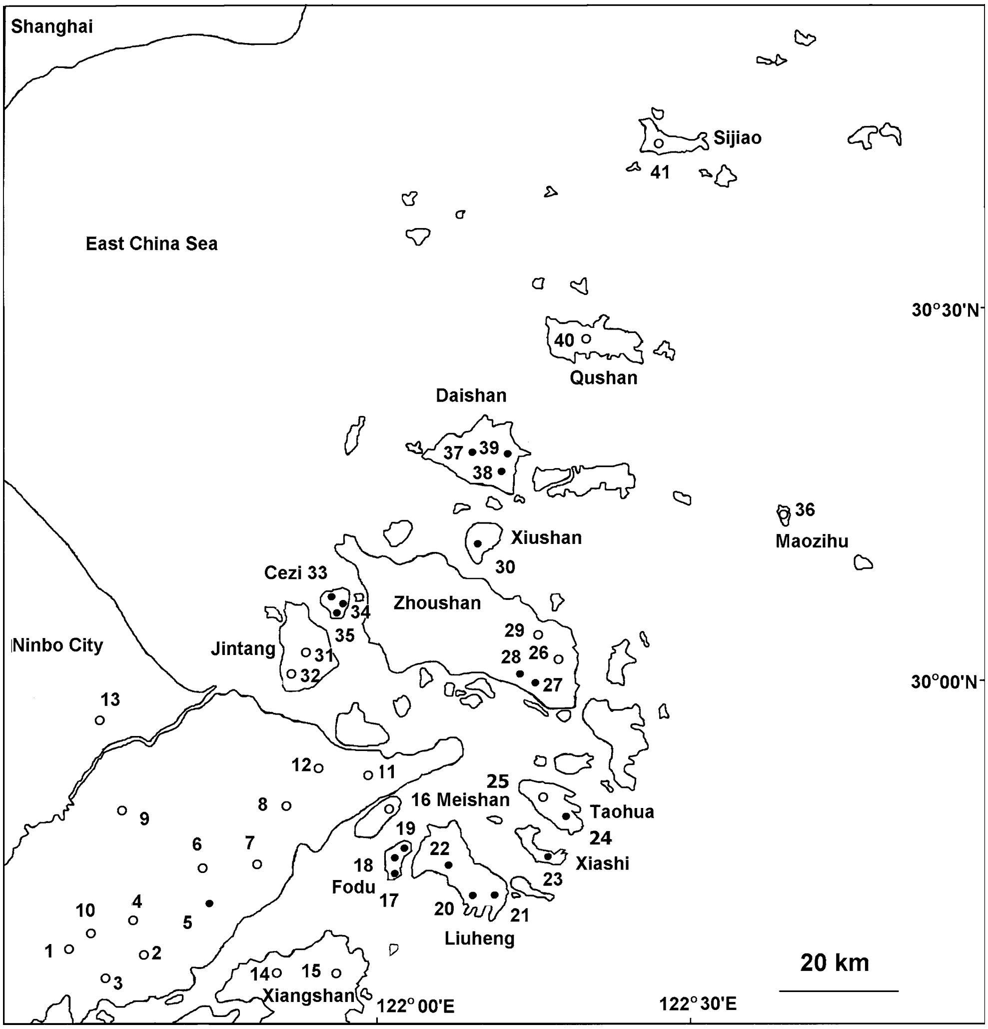

Fig. 1 Locations of farms investigated with success (*filled circle*) or failure (*open circle*) of bullfrog (*Rana catesbeiana*) invasion in establishing a reproducing population in Zhoushan archipelago and neighboring mainland, Zhejiang province of China. Forty-one farms were investigated: from one to 13 in Ninbo City and 14–15 in Xiangshan County on the mainland, 17–19 in Fodu, 21–23 in Liuheng, 23 in Xiashi, 24–25 in Taohua, 26–29 in Zhoushan, 30 in Xiushan, 31–32 in Jintang, 33–35 in Cezi, 36 in Miaozihu, 37–39 in Daishan, 40 in Qushan and 41 in Sijiao, in the Zhoushan archipelago

fields, pools or reservoirs on their property. Enclosures ranged from 0.03 to 2 ha, but were typically around 0.13 ha in area. At the time we conducted our study most farmers had ceased raising bullfrogs for several years because of poor economic returns. We looked for such farms on 22 of the main islands of the archipelago (Jintang, Damao, Cezi, Zhoushan, Meishan, Liuheng, Fodu, Taohua, Mayi, Xiashi, Yuanshan, Huni, Xiushan, Daishan, Xiaochangtu, Qushan, Miaozhihu, Sijiao, Jinping, Huanglong, Chengshan and Huaniao), and in Ninbo City and Xiangshan County on the mainland. Some farms that used to raise bullfrogs have been converted into buildings, roads or dwelling places; we excluded these from our study and considered only farms that were still in agricultural production. We were able to find 26 farms that had raised bullfrogs on ten islands in the Zhoushan archipelago and 15 farms on the neighboring mainland (Fig. 1). We surveyed these farms in the bullfrog breeding season between the end of April and the end of June 2004. At each farm, we located a 250×250-m sampling plot centered on the bullfrog enclosure. A side of the plot was determined in parallel to a road or a river that was close to the plot. The size of the plot was dictated by the relatively small dispersal distances of most adult frogs (usually <200 m; Bury and Whelan 1985; Blaustein et al. 1994), and our observation that frogs are commonly found close to enclosures from which they escaped. We collected data on characteristics of the local habitat in each plot, the number of bullfrogs raised in the enclosure, the period during which bullfrogs had been raised, human hunting activities around the enclosures, bullfrog invasion success and native frog species richness in every plot.

Habitat characteristics

Habitat characteristics of each plot were measured during the daytime. We determined the area and maximum depth of permanent water (including rivers, streams, pools and reservoirs) as an indication of the extent of suitable frog habitat in each plot. The cover of submersed vegetation in a 3-m-wide strip from the edge of permanent water was recorded in one of ten categories: 1 (0%), 2 (1–10%), 3 (11–20%),...,9 (81–90%) and 10 (>90%), and the elevation and location of the enclosure within each plot was recorded using a geographical positioning system. Most plots had only one permanent water body. For plots with more than one permanent water body, we used the maximum depth of permanent water recorded, and used the submerged vegetation cover of the water body with that maximum depth value.

Number of bullfrogs raised in an enclosure and the duration of raising

We made a questionnaire and interviewed farmers that had raised or were still raising bullfrogs on their farm, asking "how many bullfrog individuals did you usually raise and over what period were you raising bullfrogs." Many farmers provided information on the area of their enclosure and the density of bullfrogs within that area. This was converted to the total number of bullfrogs raised by multiplying the area by the density. When possible, we also measured the area of the enclosure in the field, which usually matched the information given to us by the farmers. When there was a discrepancy, we used the area we measured.

Hunting pressure

We formulated a questionnaire and met two local farmers in a village where the farms raised bullfrogs to ask "is there frog hunting activity at night in your village." One of the farmers interviewed usually was the farmer who raised bullfrogs. The other was from one of the neighboring farms, which was selected at random. In a village where there were more than one bullfrog raising farms, we still interviewed two randomly selected farmers in the village because the hunting pressure on farms was similar in the same village. We were able to interview 70 farmers in 35 villages (where 41 sampled farms were situated), including 24 farmers in 12 villages of the neighboring mainland and 46 farmers in 23 villages in the islands. The farmers are concerned about hunting activities on their farms because hunters can damage their crops, so any activity is likely to be well known. All farmers who received the questionnaire responded (i.e., response rate = 100%). The answers of the two farmers in each village were always consistent. The answers usually were "frequent hunting," or "occasional hunting" or "no hunting." While searching our plots for bullfrogs we also recorded any human hunting activity in the area. Hunters typically use electric torches to find frogs and catch them by hand or with tools. One of us approached people with lights to see if they were hunting frogs. Hunting activity was observed directly on three farms on the mainland and two farms on islands, and all answers of farmers interviewed in five villages where these farms were situated were "frequent hunting," suggesting that the "frequent hunting" was associated with higher hunting pressure. We therefore classified hunting pressure as a dichotomous variable with frequent hunting defined as situations in which farmers said that there was frequent hunting activity in the village. Other cases were defined as occasional (or no) hunting.

Bullfrog invasion success and native frog species richness

The establishment of a wild reproducing population is generally considered an indication of invasion success (Ricciardi and Atkinson 2004). Escaped and reproducing populations of bullfrogs must derive primarily from adult frogs because sub-adults are weak jumpers and could not escape over the ca. 1-m-tall enclosure fences. Consequently, any sub-adults found in the wild must derive primarily from reproduction in the wild. We defined a successful invasion as one in which there was a wild reproducing population of bullfrogs on a farm, as identified by the presence of both adult and sub-adult individuals. On Daishan, where three farms had raised bullfrogs, a wild reproducing population had spread over most of the island and it was not obvious whether the population originated from one or several of the farms. We therefore estimated the density of bullfrogs in the plots surrounding enclosures and along transects radiating out from each enclosure. In all cases, we found higher densities of bullfrogs in the plots surrounding enclosures than further out. Assuming that this reflects the spread of populations away from source areas, we judged that all three farms had been successfully invaded.

We used native frog species richness in each plot as a measure of biotic resistance to invasion by bullfrogs. Bullfrogs are more likely to compete for food and habitat with native frogs (as opposed to other amphibians) because they have a similar life history, diet and habitat use (Wu et al. 2004). We determined that a population of a native frog species was present in a plot if at least one male (or call of a male) and one female were found in the plot.

Three investigators simultaneously sampled one plot per night. The plot was divided into three equal parts and each investigator surveyed on one of the parts. The investigators kept at the same distance and same pace and were parallel to carefully search for frogs in the plot from one side to other, between 1900 and 2130 hours using electric torches (12-V DC lamp). All habitats, including pools, puddles, rivers, reservoirs, streams and banks, grassland, shrubland, forest, rice fields and non-irrigated farmland in a plot, were systematically searched by following transects along all available water courses and searching at a speed of 1.5–2 km/h. For reservoirs, pools, puddles and streams, the transects followed the accessible shoreline. For rice fields, the transects followed the edge of the field. For non-irrigated farmland, grassland, shrub and forest, the transects followed ditches or drains within each of these habitats.

Frog species were identified by sight and call with the help of guidebooks (Huang 1990), and some specimens were collected to confirm identifications (Huang 1990). Because the aim of the survey was to determine bullfrog invasion success and native frog species richness, when investigators confirmed that a species had a population in a plot (a male and a female found for the species), they did not record additional individuals of that species. Instead, they put their effort into searching for other species. Hence, 1 night's searching was sufficient to record all native frog species present in a plot at the time.

Statistical analysis

Area of permanent water and number of bullfrogs raised were $\log_{10}$ transformed for analysis. We first compared differences in invasion success between islands and mainland, along with characteristics of island and mainland farms that could potentially affect invasion success using *t*-tests (for continuous variables) and χ^2-tests of independence (for categorical variables). We then identified which characteristics could explain significant variation in invasion success by fitting logistic regression models with invasion success as the binary response variable and number of bullfrogs raised, duration of raising, year raising ceased, hunting pressure, vegetation cover, area and depth of permanent water and native frog species richness as explanatory variables. Initially, we fitted models in which each explanatory variable was included alone, and then fitted a multiple regression model in which all explanatory variables were included and the model was simplified by backward stepwise selection, retaining only those variables that independently explained significant variation in invasion success (as assessed by Akaike's information criteria values when the variables were removed from the model). The data we used are included in Appendix 1. All analyses were done using R v2.1.1 ® Development Core Team 2005), and for all comparisons the significance level is 0.05.

Results

We found both adult and sub-adult bullfrogs in the wild on 18 farms, including one farm on the mainland and 17 farms on eight islands in the Zhoushan archipelago. It was clear that wild reproducing populations of bullfrogs had established on these 18 farms and we did not see any individuals of bullfrogs on other farms. The success of bullfrog invasion on islands (17/26) was significantly higher than on the adjacent mainland (1/15; see Table 1). Farms located on islands also differed significantly from those on the mainland in several other respects: they tended to have raised fewer bullfrogs for a shorter duration, they were less likely to have hunting activity, and native frog species richness was lower on islands than the mainland (Table 1).

When included alone in logistic regression models, three factors explained significant variation in invasion success: farms were more likely to be invaded if they had occasional or no hunting relative to frequent hunting activity, if they had a greater area of permanent water, and if they had lower native frog species richness (Table 2). Two factors were retained in the stepwise logistic regression model: hunting pressure and the number of bullfrogs raised (Table 2). The form of these relationships is summarized in Table 3. As before, farms with frequent hunting activity were less likely to be successfully invaded (3/20) than farms with occasional or no hunting activity (15/21). Within each of the hunting pressure categories, farms that raised a greater number of bullfrogs were also more likely to be invaded.

There is a potential problem with non-independence in these data because some islands had more than one farm and the outcome for farms on the same island may be correlated due to unmeasured island-level features that affect invasion success. To control for this, we fitted a generalized linear mixed model with hunting pressure and number of bullfrogs raised as fixed explanatory variables and a variable coding for island identity (with mainland farms coded as one island) as a random effect. Both hunting pressure and number of bullfrogs raised were significant in this model, implying that our results are robust to the potential problem of non-independence due to the clustering of farms by island.

Differences in hunting pressure and number of bullfrogs raised largely explained the difference in invasion success between island and mainland locations. While a variable coding for island or mainland was highly significant when included alone in a logistic regression model [likelihood ratio test (LRT) = 15.3, $P < 0.0001$], its significance was much reduced when included in a multiple regression model along with hunting pressure and number of bullfrogs raised (LRT = 3.2, $P = 0.07$). Furthermore, within the 26 farms on the Zhoushan archipelago, both hunting pressure and number of bullfrogs raised were retained as predictors in multiple stepwise regression (LRT = 4.0 and 6.2, $P = 0.045$ and 0.013, respectively), suggesting these factors explain variation in invasion success within islands, as well as between island and mainland locations.

Discussion

Several of our findings confirmed predictions of the biotic resistance hypothesis. First, bullfrog invasion success was greater on islands than the mainland. Second, native frog species richness was lower on islands than the mainland. Third, native frog species richness explained significant variation in bullfrog invasion success when included alone in a logistic regression model. Nevertheless, our results show that farms on island and mainland locations differed in several other respects,

Table 1 Comparison of bullfrog invasion success and characteristics of the farms used to raise bullfrogs between islands in the Zhoushan archipelago and the neighboring mainland, Zhejiang province, China. Values are proportions or means (SE)

	Island	Mainland	Test[a]
Proportion of successful invasions	17/26	1/15	13.3***
Log_{10}(number of bullfrogs raised)	3.4 (0.12)	3.8 (0.12)	2.2*
Duration of raising (years)	2.4 (0.33)	3.7 (0.63)	2.1*
Year raising ceased	1997 (0.60)	1997 (0.16)	0.0
Proportion frequently hunted	5/26	15/15	24.8***
Vegetation cover (category)[b]	4.3 (0.48)	4.1 (0.42)	0.4
Log_{10}(area of permanent water)	3.0 (0.12)	2.7 (0.09)	1.5
Permanent water max. depth (m)	1.5 (0.23)	1.1 (0.10)	1.5
Native frog species richness	4.2 (0.19)	5.7 (0.16)	5.2***

*$P < 0.05$, ***$P < 0.001$

[a] t-values from a comparison of the means for continuous variables, and χ^2-values from a test of independence for categorical variables (proportion of successful invasions and proportion frequently hunted), with significance determined by 2,000 random reshufflings of the data due to low cell counts

[b] Category is the unit for vegetation cover (see text)

Table 2 Results of logistic regression models with bullfrog invasion success as the response variable and the variables in the first column as explanatory variables. β Parameter estimate, *LRT* likelihood ratio statistic testing the significance of a variable in the model, *ONH* occasional or no hunting, *FH* frequent hunting

Explanatory variable	Alone[a]			Multiple[b]		
	β	SE	LRT	β	SE	LRT
Log_{10}(number of bullfrogs raised)	0.09	0.55	0.03	1.55	0.79	4.5*
Duration of raising (years)	−0.12	0.17	0.6			
Year raising ceased	0.02	0.09	0.04			
Proportion frequently hunted						
ONH	2.65	0.79	14.2***	3.65	1.03	18.7***
FH	0	–	–	0	–	–
Vegetation cover (category)[c]	−0.03	0.15	0.04			
Log_{10}(area of permanent water)	1.32	0.70	4.3*			
Permanent water max. depth (m)	0.54	0.37	2.5			
Native frog species richness	−0.62	0.32	4.3*			

*$P < 0.05$, ***$P < 0.001$

[a] Results of logistic regression models when each explanatory variable was included on its own

[b] Results from a stepwise logistic regression model (see text)

[c] Category is the unit for vegetation cover (see text)

most notably that mainland farms were more likely to have frequent frog hunting activity. Furthermore, hunting activity was a much stronger predictor of bullfrog invasion success than native frog species richness for island and mainland locations combined and for islands alone, with native frog species richness excluded from both multiple regression models. Hence, our results imply that hunting pressure is an important determinant of bullfrog invasion success and that the ease with which bullfrogs have invaded islands has little to do with biotic resistance but results primarily from less hunting activity on islands compared to the mainland.

We did not measure native frog abundance on the farms under study, which, it could be argued, may affect bullfrog invasion success. However, current native frog abundance on the study farms would not provide an independent measure of invasion resistance because bullfrogs can reduce native frog abundance in areas they invade (Moyle 1973; Bury and Luckenbach 1976; Fisher and Shaffer 1996; Kiesecker and Blaustein 1997;

Table 3 The number of farms and the mean of log_{10}(number of bullfrogs raised) classified by invasion outcome and hunting pressure. For abbreviations, see Table 2

Invasion outcome	FH		ONH	
	Number of farms	Mean number of bullfrogs raised (SE)	Number of farms	Mean number of bullfrogs raised (SE)
Failed	17	3.77 (0.12)	6	3.02 (0.40)
Successful	3	4.15 (0.30)	15	3.50 (0.05)

Kupferberg 1997; Kats and Ferrer 2003). Ideally we would have measured native frog abundance on farms prior to bullfrog introductions, but such data are not available. Furthermore, to explain the observed differences in island–mainland invasibility, we would expect native frog abundance to be higher on mainland compared to island locations. In fact, native frog abundance (density) on islands is generally equal to or greater than that of mainland locations (Wu 2005).

Lower hunting pressure on islands is due to smaller human populations and less demand for frog food over much of the archipelago. Most frog hunting is done to capture frogs for sale in larger towns or cities where the demand for frog food is high. Compared with the mainland or larger islands, small islands have relatively small human populations and thus a lower demand for frog food. Furthermore, it is not economically viable to hunt frogs on small islands and then transport them to larger towns or cities. Thus, higher frog hunting pressure occurs mainly on larger islands, such as Zhoushan, Jingtang and Qushan, but not on smaller islands (see Appendix 1). Hunting on large islands and the mainland is likely to reduce invasion success for two reasons. First, it will reduce (or possibly eliminate) the population, and smaller populations will then be prone to extinction due to demographic or environmental stochasticity (Goodman 1987; Lande 1993). Second, hunting targets adult frogs, with adult male bullfrogs being especially easy to catch by call identification in the field. Selective predation on adults is likely to markedly lower fecundity and population growth rate such that invasive bullfrogs in the wild may have difficulty establishing or maintaining a reproducing population under frequent hunting.

Having controlled for differences in hunting activity, farms were more likely to be invaded if they had raised a greater number of bullfrogs, implying an important role for propagule pressure. Hence, our results confirm a general finding that the number of introduced individuals is an important factor determining the success or failure of animal invasions (insects: Beirne 1975; Ehler and Hall 1982; Hopper and Roush 1993; Berggren 2001; birds: Griffith et al. 1989; Veltman et al. 1996; Wolf et al. 1998; Duncan 1997; mammals: Crowell 1973; Ebenhard 1988; Griffith et al. 1989; Wolf et al. 1998; Forsyth and Duncan 2001). In this case, variation in propagule pressure cannot explain the higher bullfrog invasion success on islands because farms on islands tended to raise fewer bullfrogs and for a shorter duration than farms on the mainland (Table 1).

Several studies have suggested that habitat suitability or quality may play a role in invasion success (Griffith et al. 1989; Wolf et al. 1998; Blackburn and Duncan 2001). None of the habitat characteristics we measured explained significant variation in invasion outcomes possibly because all farms contained suitable bullfrog habitat. Bullfrogs have flexible habitat and food requirements: the basic condition for survival is permanent water (Bury and Whelan 1985) that was present on all farms. Moreover, the bullfrogs large body size and longevity (Bury and Whelan 1985) mean they are probably buffered from environmental extremes, characters that may contribute to their success as invaders worldwide.

An emerging number of studies are revealing that, relative to biological and ecological factors, factors either directly or indirectly under human control can explain much of the variation in the outcome of biological invasions (see reviews in Kolar and Lodge 2001; Duncan et al. 2003). This study reinforces this finding. It appears that factors under human control (level of human hunting pressure and the numbers of frogs raised in enclosures) are strong determinants of bullfrog invasion success and can account for the observed differences in invasibility between islands in the Zhoushan archipelago and neighboring mainland locations.

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