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# Life-history traits associated with fragmentation vulnerability of lizards in the Thousand Island Lake, China

Y. Wang<sup>1</sup>, J. Zhang<sup>1</sup>, K. J. Feeley<sup>2</sup>, P. Jiang<sup>1</sup> & P. Ding<sup>1</sup>

<sup>1</sup> College of Life Sciences, Zhejiang University, Hangzhou, China

<sup>2</sup> Biology Department, Wake Forest University, Winston-Salem, NC, USA

## Keywords

faunal relaxation; fragmentation vulnerability; habitat fragmentation; life-history traits; lizards; natural density; Thousand Island Lake.

## Correspondence

Ping Ding, College of Life Sciences, Zhejiang University, Zijingang Campus, Hangzhou 310058, China. Tel: +86 571 88206468  
Email: dingping@zju.edu.cn

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## Abstract

Following habitat fragmentation, the remnant faunal community will undergo a period of species loss or 'relaxation.' Theory predicts that species with particular life-history traits, such as a small population size, small geographical range, low fecundity and large body size, should be more vulnerable to fragmentation. In this study, we investigated the relationships between the above life-history traits and the fragmentation vulnerability index (the number of islands occupied) of five lizard species inhabiting recently isolated land-bridge islands in the Thousand Island Lake, China. Data on life-history traits were collected from field surveys (population density) and from the literature (body size, clutch size and geographical range size). The species–area relationships for lizards sampled from the mainland versus on the islands differed significantly (i.e. the number of species inhabiting islands was decreased relative to similar-sized areas on the mainland), indicating that species extinction has occurred on all of the study islands following isolation. For the fragmentation vulnerability index, model selection based on Akaike's information criterion identified natural density at mainland sites as the best correlate of vulnerability to fragmentation, supporting the hypothesis that rare species are most vulnerable to local extinction and will be lost first from fragmented landscapes. In contrast, there was little evidence for an effect of lizards' snout–vent length, clutch size or geographical range size on fragmentation vulnerability. Identification of species traits that render some species more vulnerable to fragmentation than others has important implications for conservation and can be used to aid direct management efforts.

## Introduction

Habitat fragmentation is widely considered to be one of the greatest threats to biological diversity (Wilcove *et al.*, 1998). Many studies have shown that following fragmentation, the faunal community will undergo a period of species loss, or 'relaxation,' before a new equilibrium community is established (MacArthur & Wilson, 1967; Diamond, 1972; Terborgh, 1974; Ferraz *et al.*, 2003). However, because large-scale planned experiments are usually constrained by laws, ethical considerations and logistic and scientific obstacles, the processes and mechanisms underlying species loss remain poorly understood (Robinson *et al.*, 1992; Debinski & Holt, 2000; Haila, 2002). In light of these difficulties, large-scale 'unplanned natural experiments' (Diamond, 2001) such as the islands created by the inundation of hydroelectric reservoirs at Gatun Lake, Panama and Lake Guri, Venezuela, have provided invaluable opportunities to examine the processes and mechanisms driving local species extinctions (Terborgh, Lopez & Tello, 1997; Diamond, 2001; Wu *et al.*, 2003).

Theory predicts that species with particular traits, such as a small population size, small geographical range, low fecundity and large body size, may be at a greater risk of extinction than others (McKinney, 1997; Simberloff, 1998; Purvis *et al.*, 2000). First, small populations are more likely to die out than large ones because small populations are vulnerable to demographic and environmental stochasticity, genetic deterioration, inbreeding and slow rates of adaptation (Pimm, Jones & Diamond, 1988; Pimm, 1991; Lande, 1999). Second, a small geographic range is commonly viewed as one form of rarity (Rabinowitz, Cairns & Dillon, 1986) and thus may likewise increase the risk of extinction by reducing the likelihood of population persistence in the face of problems caused by demographic stochasticity, local catastrophes and/or inbreeding (Gaston, 1994; Angermeier, 1995; Purvis *et al.*, 2000; Jones, Purvis & Gittleman, 2003). Moreover, species with low fecundity are also predicted to be at a greater risk of extinction than those with high fecundity because they will be less able to compensate for any increase in mortality (MacArthur & Wilson, 1967),

extending the time needed to recover from population ‘crashes’ and increasing the chance of stochastic extinction (Pimm *et al.*, 1988). Finally, a large body size is typically correlated with traits that promote extinction risk, such as a low population density and high rates of exploitation (McKinney, 1997; Cardillo, 2003). Therefore, large-bodied species are often quickly lost from habitat fragments. However, the relative importance of these traits is much less clear, as analyses are often confounded by a high degree of collinearity or synergistic interactions among traits (Laurance, 1991; Davies, Margules & Lawrence, 2004; Hero, Williams & Magnusson, 2005).

Lizards are well suited for evaluating vulnerability to habitat fragmentation for several reasons. First, lizards are tightly linked to their habitats (Pough *et al.*, 1998), and are thus sensitive to fragmentation (e.g. Cosson *et al.*, 1999; Mac Nally & Brown, 2001; Driscoll, 2004). Second, lizards are ecologically highly diverse, suggesting differential vulnerability contingent upon species-specific ecological traits (Pough *et al.*, 1998). Moreover, lizards are vertebrates with poor mobility compared with birds and mammals, which may increase its vulnerability to habitat fragmentation to a greater extent (Mac Nally & Brown, 2001). However, existing studies examining the effects of habitat fragmentation on vertebrates are extraordinarily biased to birds and mammals, while few studies have examined lizards and their vulnerability to habitat fragmentation (Sarre, Smith & Meyers, 1995; Mac Nally & Brown, 2001).

In this study, we investigated the effects of habitat fragmentation on lizard species using data from islands created by the inundation of Thousand Island Lake in Zhejiang Province, China. We first showed that species extinctions had occurred on islands by comparing the species–area relationships (SPARs) for lizards in the Thousand Island Lake with that in the neighboring mainland. We then test *a priori* four well-defined and commonly cited hypotheses that species with a small population size, a small geographical range, a low fecundity and a large body size would be more vulnerable to fragmentation. Understanding the relationships between species traits and fragmentation vulnerability will have important implications for conservation, improving predictions about which species are most threatened by future disturbances and helping to direct management efforts.

## Methods

### Study sites

The Thousand Island Lake (29°22′–29°50′N, 118°34′–119°15′ E) was created in 1959 by the damming of the Xinanjiang River in western Zhejiang Province for the purpose of generating hydroelectricity (Fig. 1). With construction of the Xinanjiang dam, an area of *c.* 580 km<sup>2</sup> was inundated, creating 1078 islands (0.25–1320 ha) out of former hilltops when the waters reached their final level (108 m). The natural vegetation of the area is a mix of subtropical deciduous and coniferous forest. The shrubs on

most islands are very dense, and are composed of *Smilax davidiana*, *Grewia biloba*, *Rhamnus utilis*, *Vaccinium henryi*, *Eurya muricata*, *Lespedeza virgata*, *Loropetalum chinense*, etc. (Sun *et al.*, 2008). The climate is typical of the subtropical monsoon zone and is highly seasonal, with hot summers and cold winters. The average annual temperature is 17.0 °C, ranging from –7.6 °C in January to 41.8 °C in July. Annual precipitation at the study sites is 1430 mm.

We conducted our research across a set of 42 islands and seven neighboring mainland sites. Study islands were selected to represent a range of areas and degrees of isolation (Table 1). Island sizes were measured by polar planimetry as the total island areas in hectares. Distances from the mainland and among the islands (the source areas for small islands were deemed the nearest large island or the mainland) were estimated from a map at a scale of 1:10 000. We selected seven nearby mainland ‘control’ sites that were located on a peninsula that juts into the lake. We selected this situation to mimic as closely as possible the physical conditions characteristic of islands (exposure to edge and prevailing easterly winds).

### Sampling methods

We used the line transect method (Jaeger, 1994) to survey lizard occupancy and abundance on each of the study islands and mainland sites during two breeding seasons between 16 April and 30 July in 2007 and 2008. To facilitate surveys, we cut transect trails (*c.* 20 cm wide) that traversed the mountain ridges on all the islands and at the mainland control sites (Terborgh *et al.*, 1997). As the cut transect trails were very narrow (*c.* 20 cm wide), and none of the five lizard species prefers open areas (Huang, 1990), the cutting of transects may not be relevant to our study species. To account for the greater habitat diversity associated with larger sites, sampling effort was roughly proportional to island area ( $\log_{10}$  transformed) (Schoederer *et al.*, 2004). Accordingly, eight transect trails were sampled on island 1 (the largest study island, area > 1000 ha), four on islands 2 and 3 (island area > 100 ha), two on four islands (10 < island area < 100 ha) and one on each of the remaining small islands (island area < 10 ha; Table 1). Consequently, larger sites were sampled more intensively on an absolute basis but less intensively per unit area than smaller sites.

During the survey, an observer walked each transect trail at a steady pace (10 m min<sup>-1</sup>) searching the ground and on tree boles with PANDA<sup>®</sup> 10 × 40 roof prism binoculars. Any lizards detected within 4 m of the trails were recorded. Once a lizard was detected, the time spent in identification (if necessary) was excluded from the elapsed survey time; only individuals for which confident identifications could be made (using the criteria of Stebbins, 2003) were included in analyses (Germaine & Wakeling, 2001). We used GPS to record the length of each line transect. Surveys were conducted from between 1 h after sunrise until 5 h after sunrise. All the islands were surveyed 20 times. The order in which islands were surveyed and the direction in which the trails were walked were alternated in order to minimize potential



**Figure 1** Locations of study sites (highlighted in black) in the Thousand Island Lake and on the neighboring mainland, Zhejiang Province, China. Island numbers refer to the information in Table 1. S1–S7 present mainland study sites.

biases. Censuses were not conducted during inclement weather such as strong winds or rains.

A similar sampling method was used on the mainland as on the islands. To determine the distribution of lizard species in the unfragmented habitats, we cut seven trails (c. 20 cm wide) that were 20, 40, 80, 100, 200, 400 and 800 m long in the seven sites, respectively. Any lizards detected within 4 m of the trails were recorded. As on the islands, each mainland site was surveyed 20 times.

### Life-history traits

We collected published data on the geographical range size, body size and clutch size for all five lizard species inhabiting the study islands. We used snout–vent length (SVL) as the body size. Following Jones *et al.* (2003), the geographic range size (km<sup>2</sup>) was obtained from the most recent available published species range maps by digitizing the area into a Geographic Information System (ArcView 3.2). Where no range maps were available, the minimum area convex polygon of published point data was calculated excluding areas of water. All these life-history data were taken from

Huang (1990), Zhao & Adler (1993), and China Wildlife Conservation Association (2002), except for the clutch size of *Scincella modesta*, which was not described in these publications, and was obtained from Feng (1991). If a range instead of the mean SVL or clutch size was provided in the literature, we used the arithmetic mean of the limits (Gaston & Blackburn, 1995).

Natural density was calculated for each species based on the results of the transect surveys at mainland sites (Meyer *et al.*, 2008). For each species, we first calculated the population density per transect by dividing average number of detections per transect by transect length in each transect. We then calculated the population density for each species by averaging the densities among transects. The insular population density of each species was calculated similarly, but including only those islands on which the species was detected (Crooks *et al.*, 2001).

### Statistical analyses

In order to determine whether species extinctions had in fact occurred on the islands, we compared the log<sub>10</sub>–log<sub>10</sub> SPAR

**Table 1** Distribution of lizard species on 32 islands in the Thousand Island Lake, China [+ , presence of a species on the island, *Euch*, *Eumeces chinensis*; *Tase*, *Takydromus septentrionalis*; *Euel*, *Eumeces elegans*; *Scmo*, *Scincella modesta*; *Spin*, *Sphenomorphus indicus*; *S*, species richness (numbers in parentheses are average species richness per transect controlled for sampling effort); area, island area (ha); distance from mainland, distance from the nearest mainland (m); distance from larger island, distance from the nearest larger island (m); sampling area, transect length  $\times$  transect width (4 m)]

Island	Lizard species						S	Area	Distance from		Number of transects ( <i>n</i> )	Total length of transects (m)	Sampling area (ha)
	<i>Euch</i>	<i>Tase</i>	<i>Euel</i>	<i>Scmo</i>	<i>Spin</i>	Mainland			Larger island				
1	+	+	+	+	+	5 (4.0)	1289.23	897.41	897.41	8	3200	1.28	
2	+	+	+		+	4 (3.5)	143.19	1415.09	786.31	4	1600	0.64	
3	+	+	+	+		4 (3.5)	109.03	964.97	132.30	4	1600	0.64	
4	+	+	+	+	+	4 (3.0)	55.08	953.95	506.00	2	800	0.32	
5	+	+	+	+		4 (3.0)	35.64	2110.41	34.16	2	800	0.32	
6	+	+	+			3 (3.0)	46.37	729.80	155.35	2	800	0.32	
7	+	+		+		3 (2.5)	32.29	1936.95	470.87	2	800	0.32	
8	+	+				2	5.69	21.85	379.46	1	375	0.15	
9	+		+			2	2.83	1238.14	154.60	1	150	0.06	
10	+		+			2	2.29	973.85	30.37	1	300	0.12	
11		+	+			2	2.00	1042.38	56.52	1	300	0.12	
12	+	+				2	1.74	2293.25	331.69	1	300	0.12	
13	+		+			2	1.17	2453.37	36.63	1	250	0.10	
14	+	+				2	1.20	2128.52	29.79	1	225	0.09	
15				+	+	2	1.01	2437.85	89.11	1	250	0.10	
16	+		+			2	0.73	1320.40	81.91	1	300	0.12	
17	+			+		2	0.59	1018.42	26.16	1	250	0.10	
18		+			+	2	0.30	1086.03	41.60	1	175	0.07	
19	+					1	2.90	1785.30	32.32	1	275	0.11	
20	+					1	1.93	888.05	26.32	1	250	0.10	
21	+					1	1.54	711.04	72.59	1	275	0.11	
22	+					1	1.52	849.88	60.37	1	250	0.10	
23		+				1	1.52	2849.99	90.22	1	175	0.07	
24	+					1	1.40	1760.34	100.39	1	375	0.15	
25	+					1	1.26	54.86	410.49	1	200	0.08	
26	+					1	1.20	657.72	29.80	1	225	0.09	
27	+					1	1.03	1458.81	90.72	1	250	0.10	
28		+				1	1.01	2103.85	41.05	1	250	0.10	
29		+				1	0.86	2321.51	46.65	1	225	0.09	
30		+				1	0.83	2298.50	16.74	1	275	0.11	
31	+					1	0.80	2097.52	101.43	1	300	0.12	
32	+					1	0.67	1139.87	17.01	1	325	0.13	

Other 10 study islands contain no lizard species.

generated for lizards occurring on the islands of Thousand Island Lake with the curve generated for the mainland sites. As the sampling effort on seven large islands is much higher than small islands (Table 1), this may increase the probability of detecting rare species with a low detection probability (Hill, Curran & Foody, 1994). To standardize the sampling effort in the SPAR analyses, we used the average number of species per transect instead of the total number of species recorded per island. Moreover, to standardize the SPAR comparison between islands and mainland sites, we used the sampling areas rather than island areas to make them comparable to mainland plot areas. The sampling areas were calculated as total transect length  $\times$  transect width (4 m) (Table 1).

To differentiate fragmentation effects on species diversity from area effects, we applied the SPAR method as follows

(Yaacobi, Ziv & Rosenzweig, 2007). We first determined the SPAR for lizards on islands. Then we extrapolated the SPAR to a point above the total sampling area (6.45 ha) of the set of islands. The value of diversity at that point represents the predicted value of lizards' diversity for an imaginary patch of that size, providing fragmentation has no effect on diversity. If the actual number of species in the set of 32 islands is less than this predicted value, then fragmentation will have decreased diversity. If it is greater, then fragmentation will have increased diversity. To determine whether the total species number in the set of 32 islands departs significantly from the predicted value, we examined whether it was in the 95% confidence interval of the predicted value. As the potential species pool in nearby mainland of the Thousand Island Lake is larger than the predicted value of lizards' diversity ( $11 > 10.03$ ) (Huang,

1990), the species–area curve is not saturated and meets the extrapolation assumption of the SPAR analysis.

We used the number of islands occupied by each species as the measure of fragmentation vulnerability. This index is regarded as a good predictor of extinction vulnerability (Bolger, Alberts & Soulé, 1991; Viveiros de Castro & Fernandez, 2004; Meyer *et al.*, 2008), to which it is inversely related. By considering the absence of a species in a given fragment as a local extinction, we made an important assumption that all species were present in the whole study area before the fragmentation. We think the assumption is very likely for the following reasons. First, the small spatial scale of the area: the islands were separated by only a few thousand meters within the original continuous mainland (Fig. 1). Second, all five species studied are common in continuous mainland and would not be expected to have very sparse populations before fragmentation.

In preference to traditionally applied stepwise selection procedures whose use is statistically problematic (Quinn & Keough, 2004; Whittingham *et al.*, 2006), we used an information-theoretic approach based on Akaike's information criterion (AIC) (Burnham & Anderson, 2002) to assess the associations between the fragmentation vulnerability index and life-history traits. We used the small sample version of AIC ( $AIC_c$ ) to account for the bias introduced when the sample size is small relative to the number of estimated parameters in a model (Burnham & Anderson, 2002). To calculate  $AIC_c$  for each model, we first regressed the fragmentation vulnerability index against each life-history trait separately. All models were then ranked by rescaling the  $AIC_c$  values such that the model with the minimum  $AIC_c$  had a value of 0, that is  $\Delta_i = AIC_i - AIC_{\min}$ . The difference in  $AIC_c$  values between models can be used to calculate Akaike weights ( $\omega$ ), which is the probability that the model is the best model in the set of candidate models, given the data (Burnham & Anderson, 2002). Models for which  $\Delta_i \leq 2$  are considered to have substantial support, values of 4–7 have considerably less support, while those with  $\Delta_i \geq 10$  essentially have no empirical support and can be ignored (Burnham & Anderson, 2002). We did not consider interaction effects between variables because of the limited sample size.

We performed all analyses with SPSS statistical package (SPSS Inc., 1999). All tests are two-tailed, means are given as  $\pm$  SE and statistical significance was set at  $\alpha \leq 0.05$ .

## Results

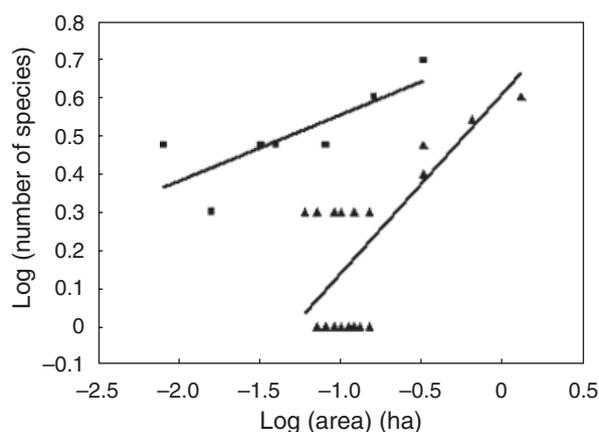
### SPAR on the mainland and in the Thousand Island Lake

A total of five lizard species were found to occur on the study islands in the Thousand Island Lake and on the neighboring mainland (Tables 1 and 2). The slopes and intercepts of the SPAR for lizards on the mainland and on the islands differed significantly ( $P < 0.05$  for both; Fig. 2). Species richness was reduced on islands relative to the mainland of the same size. This indicates that islands are

**Table 2** Distribution of lizard species in seven neighboring mainland sites of the Thousand Island Lake

Plot	Area (ha)	Lizard species					Species richness
		<i>Euch</i>	<i>Tase</i>	<i>Euel</i>	<i>Scmo</i>	<i>Spin</i>	
S1	0.008	+	+				2
S2	0.016		+			+	2
S3	0.032	+	+		+		3
S4	0.04		+	+		+	3
S5	0.08	+	+	+			3
S6	0.16	+	+	+	+		4
S7	0.32	+	+	+	+	+	5

*Euch*, *Eumeces chinensis*; *Tase*, *Takydromus septentrionalis*; *Euel*, *Eumeces elegans*; *Scmo*, *Scincella modesta*; *Spin*, *Sphenomorphus indicus*; +, the presence of a species



**Figure 2** The species–area curves for lizards on 32 islands in the Thousand Island Lake (triangles) and at seven study sites on the neighboring mainland (squares). Mainland regression equation:  $\log(\text{number of species}) = 0.733 + 0.177 \log \text{area}$ ,  $r^2 = 0.638$ ; island:  $\log(\text{number of species}) = 0.616 + 0.476 \log \text{area}$ ,  $r^2 = 0.511$ . Slopes and  $y$ -intercepts differ significantly between the mainland and islands ( $P < 0.05$ ).

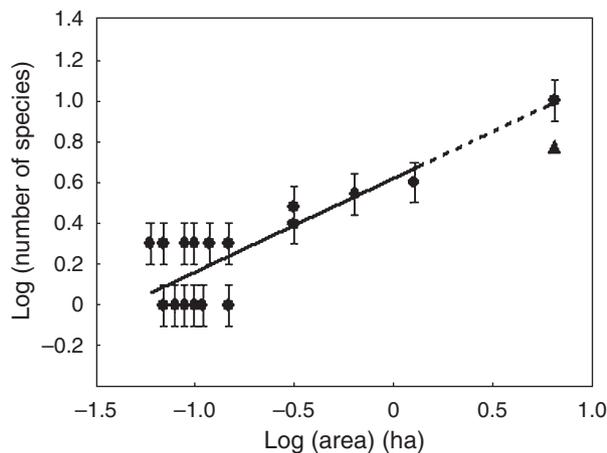
impoverished in species number relative to equal areas on the mainland. The slope of the SPAR on islands ( $Z = 0.476$ ) was considerably steeper than that of the mainland patches ( $Z = 0.177$ ), indicating that species richness increases more rapidly on the islands as a function of area than on the mainland. These differences in slope and intercept suggest that extinction of species has occurred on all islands following fragmentation but that rates of species loss were greatest on small ones.

The SPAR method showed that the set of islands had fewer lizard species than would have been present in an unfragmented area equal in size to that of the set of 32 islands ( $5 < 10.03$ ; Fig. 3). The deviation of lizard species richness from expectation departs significantly from the empirical deviation of individual islands from their species–area curve (Fig. 3), indicating that the decrease of species richness on islands was due to fragmentation effects but not area effects.

### Life-history traits and their relationships with the fragmentation vulnerability of lizards

The five lizard species occurring in the Thousand Island Lake exhibited a wide range of life-history traits (Table 3). The natural density at mainland sites varied substantially among species, *Eumeces chinensis* with the highest density and *Sphenomorphus indicus* with the lowest density. The SVL of lizards ranged from 42.36 to 91.18 mm. The clutch size of lizards ranged from 3.0 to 9.0. The geographical range size varied from 818 753 to 4 624 317 km<sup>2</sup>.

The five lizard species also exhibited considerable variations in vulnerability to fragmentation (Table 3). For the fragmentation vulnerability index (the number of islands occupied), model selection based on AIC identified natural density at mainland sites as the best single predictor of vulnerability to fragmentation for lizard species in the Thousand Island Lake (i.e.  $\omega_{\max} \geq 0.90$ ) (Table 4). There was little evidence for an effect of lizards' SVL, clutch size or geographical range size on fragmentation vulnerability ( $\Delta_i \geq 10$ ) (Table 4).



**Figure 3** Species–area relationship of the lizards (filled circle) on the 32 islands and their total number of species (filled triangle). The line shows the expected diversity if fragmentation has no effect. The error bar shows the 95% confidence interval.

### Discussion

We found that the number of lizard species inhabiting islands was decreased relative to similar-sized areas on the mainland and that the slopes and intercepts of SPARs differed between the islands and the mainland (Fig. 2), indicating that the inundation of the Thousand Islands Lake has caused the extinction of species from the newly formed islands. Many of the previous studies that have attempted to estimate the vulnerability of species to fragmentation assume that all species are present in each fragment at creation, and consequently that any species absent from a patch has become extinct (Diamond, 1972; Wilcox, 1978; Soulé *et al.*, 1988). However, this approach potentially overestimates rates of extinction since all species are not necessarily present in each fragment pre-isolation (Bolger *et al.*, 1991). Here, we accounted for this potential bias by constructing a mainland species–area curve that we then used to estimate the number of lizard species lost from the study islands (Diamond, 1984).

To date, existing studies examining the effects of habitat fragmentation on vertebrates are extraordinarily biased taxonomically (Mac Nally & Brown, 2001). Among vertebrates, birds and mammals are predominantly studied, while few studies have examined the effects of habitat fragmentation on lizards and its vulnerability to habitat fragmentation (Sarre *et al.*, 1995; Mac Nally & Brown, 2001; but see Hoehn, Sarre & Henle, 2007 for reviews). Our study on lizards thus fills in a significant gap, and contributes to the ecological generality of habitat fragmentation across a range of terrestrial vertebrate taxa.

We found that natural density at mainland sites was the best single predictor of fragmentation vulnerability for lizards in the Thousand Island Lake. This result supports the hypothesis that species occurring naturally at low densities are more prone to extinction than those occurring at a high density (e.g. Diamond, Bishop & van Balen, 1987; Robinson & Quinn, 1988). In view of the short time isolation of 50 years for the Thousand Island Lake, inbreeding, genetic deterioration and slow rates of adaptation may probably be the processes that render small lizard populations particularly vulnerable to fragmentation because these processes typically influence populations shortly after fragmentation (Pimm *et al.*, 1988; Pimm, 1991; Lande, 1999;

**Table 3** Fragmentation vulnerability index (number of islands occupied) and four life-history traits of the five lizard species inhabiting the study islands in the Thousand Island Lake

Species	Number of islands occupied ( <i>n</i> )	Natural density ( <i>n</i> ha <sup>-1</sup> )	Snout–vent length (mm)	Clutch size ( <i>n</i> )	Geographical range size (km <sup>2</sup> )
<i>Eumeces chinensis</i>	25	29.63 ± 23.92	91.18	9.0	2 525 742
<i>Takydromus septentrionalis</i>	16	25.48 ± 16.85	66.00	3.0	3 108 760
<i>Eumeces elegans</i>	10	14.69 ± 11.80	70.55	7.5	2 691 342
<i>Scincella modesta</i>	7	8.26 ± 5.96	42.36	6.0	818 753
<i>Sphenomorphus indicus</i>	5	6.25 ± 3.31	71.68	7.5	4 624 317

Sample size for natural density (mean ± SE) is the number of plots in which each species is present, refers to Table 2.

**Table 4** Results of Akaike information criterion (AIC)-based model selection assessing the association between the fragmentation vulnerability index (number of islands occupied) and a set of candidate models

Response variable	Model description	Log ( <i>L</i> )	<i>K</i>	AIC <sub>c</sub>	Δ <sub><i>i</i></sub>	ω <sub><i>i</i></sub>
Number of islands occupied	Natural density ( <i>n</i> ha <sup>-1</sup> )	-3.36	3	36.72	0	0.9897
	Snout-vent length (mm)	-8.27	3	46.54	9.82	0.0073
	Clutch size ( <i>n</i> )	-9.83	3	49.65	12.93	0.0015
	Geographical range size (km <sup>2</sup> )	-9.86	3	49.72	13.00	0.0015

For each model, the log-likelihood (Log *L*), number of estimable parameters (*K*), sample-size adjusted AIC, Akaike differences (Δ<sub>*i*</sub>) and Akaike weights (ω<sub>*i*</sub>) are presented.

Hoehn *et al.*, 2007). Natural density has also been found to be an important factor influencing the persistence of a variety of taxa in other ecosystems (Soulé *et al.*, 1988; Foufopoulos & Ives, 1999; Feeley *et al.*, 2007).

Contrary to our predictions, we found no relationships between fragmentation vulnerability and body size, fecundity or geographical range size. In contrast, previous studies have typically found that species with a small body size, high fecundity and large geographic ranges are less prone to extinction following fragmentation (e.g. Cardillo, 2003; Hero *et al.*, 2005; Cooper *et al.*, 2008). However, it is important to note two caveats associated with our study. First, we have a small sample size for studying life-history traits correlated with fragmentation vulnerability compared with other relevant studies (Foufopoulos & Ives, 1999; Hero *et al.*, 2005; Cooper *et al.*, 2008). Second, the lizard species had a very small range in SVL (42.36–91.18), clutch size (3.0–9.0) and geographical range size (818 753–3 108 760), while the ranges are much larger in other relevant studies for SVL (11.00–245.00), clutch size (3.0–25 644.0) and geographical range size (1–12 481 500) (Hero *et al.*, 2005; Cooper *et al.*, 2008). Such differences in sample size and range in life-history traits may possibly explain the differences between our results and other relevant studies.

Based on our results, natural density at mainland sites is the only species trait associated with the fragmentation vulnerability of lizards in the Thousand Island Lake, alone explaining over 90% of variation in fragmentation vulnerability among the study species. Other species traits such as habitat specificity, trophic guild and dispersal ability have also been identified as potential factors influencing fragmentation vulnerability in other systems (McKinney, 1997; Purvis *et al.*, 2000; Henle *et al.*, 2004; Hoehn *et al.*, 2007). These traits may account for some of the remaining variation in fragmentation vulnerability among lizard species and warrant further study.

Identifying traits that predispose species to extinction following fragmentation has important implications for proactive conservation and can be used to help direct management efforts. Our study showed that natural density at mainland sites was the key trait associated with the fragmentation vulnerability in lizards in the Thousand Island Lake, while lizards' body size, clutch size or geographical range size had little effects on fragmentation vulnerability. Therefore, lizard species with different extinction-proneness traits should be given different conservation

priority. As neither large lizard species nor those with low fecundity or a small range size appear to be at a particular risk of extinction, it would be inefficient to allocate conservation resources on the basis of these life-history traits. In contrast, conservation efforts giving priority to rare species with low densities may prove effective for the preservation of lizard species in this system.

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## References

- Angermeier, P.L. (1995). Ecological attributes of extinction-prone species: loss of fresh water fishes in Virginia. *Conserv. Biol.* **9**, 143–158.
- Bolger, D.T., Alberts, A.C. & Soulé, M.E. (1991). Occurrence patterns of bird species in habitat fragments: sampling, extinction, and nested species subsets. *Am. Nat.* **137**, 155–166.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and inference: a practical information-theoretic approach*. New York: Springer.
- Cardillo, M. (2003). Biological determinants of extinction risk: why are smaller species less vulnerable? *Anim. Conserv.* **6**, 63–69.
- China Wildlife Conservation Association. (2002). *Atlas of reptiles of China*. Zhengzhou: Henan Science and Technology Publishing House (in Chinese).
- Cooper, N., Bielby, J., Thomas, G.H. & Purvis, A. (2008). Macroecology and extinction risk correlates of frogs. *Global Ecol. Biogeogr.* **17**, 211–221.
- Cosson, J.F., Ringuelet, S., Claessens, O., Massary, J.C., Dalecky, A., Villiers, J.F., Granjon, L. & Pons, J.M.

- (1999). Ecological changes in recent land-bridge islands in French Guiana, with emphasis on vertebrate communities. *Biol. Conserv.* **91**, 213–222.
- Crooks, K.R., Suarez, A.V., Bolger, D.T. & Soulé, M.E. (2001). Extinction and colonization of birds on habitat islands. *Conserv. Biol.* **15**, 159–172.
- Davies, K.F., Margules, C.R. & Lawrence, J.F. (2004). A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology* **85**, 265–271.
- Debinski, D.M. & Holt, R.D. (2000). A survey and overview of habitat fragmentation experiments. *Conserv. Biol.* **14**, 342–355.
- Diamond, J.M. (1972). Biogeographic kinetics: estimation of relaxation times for avifaunas of Southwest Pacific islands. *Proc. Natl. Acad. Sci. USA* **69**, 3199–3203.
- Diamond, J.M. (1984). “Normal” extinctions of isolated populations. In *Extinction*: 191–246. Nitecki, M.H. (Eds). Chicago: University of Chicago Press.
- Diamond, J.M. (2001). Dammed experiments. *Science* **294**, 1847–1848.
- Diamond, J.M., Bishop, K.D. & van Balen, S. (1987). Bird survival in an isolated Javan woodland: island or mirror? *Conserv. Biol.* **1**, 132–142.
- Driscoll, D.A. (2004). Extinction and outbreaks accompany fragmentation of a reptile community. *Ecol. Appl.* **14**, 220–240.
- Feeley, K.J., Gillespie, T.W., Lebbin, D.J. & Walter, H.S. (2007). Species characteristics associated with extinction vulnerability and nestedness rankings of birds in tropical forest fragments. *Anim. Conserv.* **10**, 493–501.
- Feng, Z.J. (1991). Preliminary studies on *Scincella modesta* in Luojia Mountain. *Chin. J. Zool.* **28**, 6–8 (in Chinese with English abstract).
- Ferraz, G., Russell, G.J., Stouffer, P.C., Bierregaard, R.O., Pimm, S.L. & Lovejoy, T.E. (2003). Rates of species loss from Amazonian forest fragments. *Proc. Natl. Acad. Sci. USA* **100**, 14069–14073.
- Foufopoulos, J. & Ives, A.R. (1999). Reptile extinctions on land-bridge islands: life history attributes and vulnerability to extinction. *Am. Nat.* **153**, 1–25.
- Gaston, K.J. (1994). *Rarity*. London: Chapman & Hall.
- Gaston, K.J. & Blackburn, T.M. (1995). Birds, body size and the threat of extinction. *Philos. Trans. Roy. Soc. Lond. B* **347**, 205–212.
- Germaine, S.S. & Wakeling, B.F. (2001). Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. *Biol. Conserv.* **97**, 229–237.
- Haila, Y. (2002). A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecol. Appl.* **12**, 321–334.
- Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004). Predictors of species sensitivity to fragmentation. *Biodivers. Conserv.* **13**, 207–251.
- Hero, J.M., Williams, S.E. & Magnusson, W.E. (2005). Ecological traits of declining amphibians in upland areas of eastern Australia. *J. Zool. (Lond.)* **267**, 221–232.
- Hill, J.L., Curran, P.J. & Foody, G.M. (1994). The effects of sampling on the species–area curve. *Glob. Ecol. Biogeogr. Lett.* **4**, 97–106.
- Hoehn, M.L., Sarre, S.D. & Henle, K. (2007). The tales of two geckos: does dispersal prevent extinction in recently fragmented populations? *Mol. Ecol.* **16**, 3299–3312.
- Huang, M.H. (1990). *Fauna of Zhejiang: Amphibia, Reptilia*. Hangzhou: Zhejiang Science and Technology Publishing House (in Chinese).
- Jaeger, R.G. (1994). Transect sampling. In *Measuring and monitoring biological diversity: standard methods for amphibians*: 103–107. Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, L.C. & Foster, M.S. (Eds). Washington: Smithsonian Institution Press.
- Jones, K.E., Purvis, A. & Gittleman, J.L. (2003). Biological correlates of extinction risk in bats. *Am. Nat.* **161**, 601–614.
- Lande, R. (1999). Extinction risks from anthropogenic, ecological and genetic factors. In *Genetics and the extinction of species*: 1–22. Landweber, L.F. & Dobson, A.P. (Eds). Princeton, NJ: Princeton University Press.
- Laurance, W.F. (1991). Ecological correlates of extinction proneness in Australian tropical rain forest mammals. *Conserv. Biol.* **5**, 79–89.
- MacArthur, R.H. & Wilson, E.O. (1967). *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- Mac Nally, R. & Brown, G.W. (2001). Reptiles and habitat fragmentation in the box-ironbark forests of central Victoria, Australia: predictions, compositional change and faunal nestedness. *Oecologia* **128**, 116–125.
- McKinney, M.L. (1997). Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annu. Rev. Ecol. Syst.* **28**, 495–516.
- Meyer, C.F., Frund, J., Lizano, W.P. & Kalko, E.K.V. (2008). Ecological correlates of vulnerability to fragmentation in Neotropical bats. *J. Appl. Ecol.* **45**, 381–391.
- Pimm, S.L. (1991). *The balance of nature?* Chicago: University of Chicago Press.
- Pimm, S.L., Jones, H.L. & Diamond, J. (1988). On the risk of extinction. *Am. Nat.* **132**, 757–785.
- Pough, F.H., Andrews, R.M., Cadle, J.E., Crump, M.L., Savitzky, A.H. & Wells, K.D. (1998). *Herpetology*. New Jersey: Prentice-Hall.
- Purvis, A., Gittleman, J.L., Cowlishaw, G. & Mace, G.M. (2000). Predicting extinction risk in declining species. *Proc. Roy. Soc. B: Biol. Sci.* **267**, 1947–1952.
- Quinn, G.P. & Keough, M.J. (2004). *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press.
- Rabinowitz, D., Cairns, S. & Dillon, T. (1986). Seven forms of rarity and their frequency in the flora of the British Isles. In *Conservation biology: the science of scarcity and diversity*: 182–204. Soulé, M.E. (Eds). Sunderland, MA: Sinauer.
- Robinson, G.R., Holt, R.D., Gaines, M.S., Hamburg, S.P., Johnson, M.L., Fitch, H.S. & Martinko, E.A. (1992). Diverse and contrasting effects of habitat fragmentation. *Science* **257**, 524–526.

- Robinson, G.R. & Quinn, J.F. (1988). Extinction, turnover and species diversity in an experimentally fragmented Californian annual grassland. *Oecologia* **76**, 71–82.
- Sarre, S., Smith, G.T. & Meyers, J.A. (1995). Persistence of two species of Geckos (*Oedura reticulata* and *Gehyra variegata*) in remnant habitat. *Biol. Conserv.* **71**, 25–33.
- Schoereder, J.H., Galbiati, C., Ribas, C.R., Sobrinho, T.G., Sperber, C.F., DeSouza, O. & Lopes-Andrade, C. (2004). Should we use proportional sampling for species–area studies? *J. Biogeogr.* **31**, 1219–1226.
- Simberloff, D. (1998). Small and declining populations. In *Conservation science and action*: 116–134. Sutherland, W.J. (Eds). Oxford: Blackwell Science.
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Wrights, J., Sorice, M. & Hill, S. (1988). Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.* **2**, 75–92.
- SPSS Inc. (1999). *SPSS, version 10.0 [computer program]*. Chicago: SPSS Inc.
- Stebbins, R.C. (2003). *A field guide to western reptiles and amphibians*. 3rd edn. Boston, MA: Houghton Mifflin Co.
- Sun, Q., Lu, J., Wu, J. & Zhang, F. (2008). Effects of island area on plant species distribution and conservation implications in the Thousand Island Lake region. *Biodivers. Sci.* **16**, 1–7 (in Chinese with English Abstract).
- Terborgh, J. (1974). Preservation of natural diversity: the problem of extinction prone species. *BioScience* **24**, 715–722.
- Terborgh, J., Lopez, L. & Tello, J.S. (1997). Bird communities in transition: the Lago Guri islands. *Ecology* **78**, 1494–1501.
- Viveiros de Castro, E.B. & Fernandez, F.A.S. (2004). Determinants of differential extinction vulnerabilities of small mammals in Atlantic forest fragments in Brazil. *Biol. Conserv.* **119**, 73–80.
- Whittingham, M.J., Stephens, P.A., Bradbury, R.B. & Freckleton, R.B. (2006). Why do we still use stepwise modelling in ecology and behaviour? *J. Anim. Ecol.* **75**, 1182–1189.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998). Quantifying threats to imperiled species in the United States. *BioScience* **48**, 607–615.
- Wilcox, B.A. (1978). Supersaturated island faunas: a species–age relationship for lizards on post-Pleistocene land-bridge islands. *Science* **199**, 996–998.
- Wu, J., Huang, J., Han, X., Xie, Z. & Gao, X. (2003). Three-Gorge Dam – experiment in habitat fragmentation. *Science* **300**, 1239–1240.
- Yaacobi, G., Ziv, Y. & Rosenzweig, M.L. (2007). Habitat fragmentation may not matter to species diversity. *Proc. Roy. Soc. B: Biol. Sci.* **274**, 2409–2412.
- Zhao, E.M. & Adler, K. (1993). *Herpetology of China*. Oxford: Society for the Study of Amphibians and Reptiles.