

Research Article

Ecological Correlates of Vulnerability to Fragmentation in Snakes on Inundated Subtropical Land-Bridge Islands

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Abstract

In the face of widespread human-induced habitat fragmentation, identifying the ecological traits that predispose species to extinction following fragmentation has important implications for proactive conservation and can be used to help direct management efforts. However, previous studies examining the fragmentation vulnerability of vertebrates are extraordinarily biased toward birds and mammals, while few studies have examined snake assemblages. In this study, we determined how species traits influenced fragmentation vulnerability using snake data collected from land-bridge islands created by the inundation of the Thousand Island Lake, China. We used the line-transect method to determine the distribution of snake assemblages on 48 study islands during breeding seasons from 2009 to 2013. We used the number of islands occupied by each snake species as the fragmentation vulnerability index. We obtained four species traits from field surveys and from the literature: body size, clutch size, geographical range size and population abundance. These ecological traits were used separately and in combination to assess their associations with the fragmentation vulnerability index. Model selection based on Akaike's information criterion identified population abundance as the best correlate of vulnerability to fragmentation in snake species. In contrast, there was no evidence for an effect of body size, clutch size, geographical range size or their combinations on fragmentation vulnerability. Our results suggest that, in order to be effective, we should give priority conservation efforts to snake species with low population abundance in this system.

Keywords: Ecological Trait; Fragmentation Vulnerability; Habitat Fragmentation; Population Abundance; Proactive Conservation; Snake; Thousand Island Lake

Introduction

Human-induced habitat fragmentation is widely considered to be one of the major threats to biodiversity throughout the world [1,2,3]. Numerous studies have demonstrated that following frag-

mentation, the resident community will undergo a period of faunal relaxation before a new equilibrium community is achieved [4,5,6]. During the process of faunal relaxation, species in isolated fragments are predicted to go locally extinct in a predictable order due to differential extinction vulnerabilities [7,8,9]. Identifying ecological traits that render species vulnerable to fragmentation is an important prerequisite for the development of effective conservation strategies to minimize future biodiversity losses [10,11,12].

Theory suggests that species with particular traits, such as small population size, small geographical range, large body size and low fecundity, may be at a greater risk of extinction than others [13,14,11]. First, rarity in the form of small population size and small geographic range has been commonly viewed as good predictors of fragmentation vulnerability [15,16]. Second, large body size is often linked to increased extinction risk because it is typically correlated with traits that promote extinction risk, such as low population density, low fecundity and high rates of exploitation [13,14]. Finally, species with low fecundity are also predicted to be at a greater risk of extinction because they will be less able to compensate for any increase in mortality [4,17] extending the time needed to recover from population crashes and increasing the chance of stochastic extinction [18].

In this study, we investigated the fragmentation vulnerability of snake species on subtropical land-bridge islands created by the inundation of the Thousand Island Lake, China. We test a priori four well-defined and commonly cited hypotheses that species with small population size, small geographical range, large body size and low fecundity would be more vulnerable to fragmentation. Identification of ecological characteristics that render some species more vulnerable to fragmentation than others is vital for

understanding, predicting and mitigating the effects of habitat alteration on biodiversity [12].

Materials And Methods

Study Areas

The Thousand Island Lake (29°22'-29°50'N, 118°34'-119°15'E) is a large hydroelectric reservoir [9]. It was created in 1959 by the damming of the Xinanjiang River in western Zhejiang Province, China [19]. The construction of the Xinanjiang dam inundated an area of 573 km², creating 1078 land-bridge islands larger than 0.25 ha out of former hilltops when the water reached its final level (108 m) [20]. The total land area of the archipelago is 409 km². Forests on islands were clear cut before the creation of the dam [21]. The highest peak in the Thousand Island Lake is 405.2 m [22]. The major vegetation type on the islands is the naturally secondary forest dominated by *Pinus massoniana* [23]. 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 in the region is 1430 mm [24]. The research was conducted across a set of 48 islands. These islands were selected (1) to represent a range of area and degree of isolation from mainland (Table 1)

Island code	Island area (ha)	Isolation (m)	Number of habitats (n)	Number of transects (n)	Total length of transects (m)	Species richness (n)
1	1289.23	897.41	7	8	3200	12
2	143.19	1415.09	6	4	1600	6
3	109.03	964.97	6	4	1600	6
4	55.08	953.95	5	2	800	8
5	46.37	729.80	5	2	800	4
6	32.29	1936.95	5	2	800	5
7	5.69	21.85	3	1	375	3
8	3.42	583.00	4	1	300	2
9	2.90	1785.30	3	1	275	2
10	2.83	1238.14	4	1	150	2
11	2.29	973.85	4	1	300	1
12	2.23	3261.96	3	1	400	0
13	2.00	1042.38	3	1	300	2
14	1.93	888.05	4	1	250	2
15	1.74	2293.25	3	1	300	1
16	1.54	711.04	3	1	375	2
17	1.52	849.88	3	1	250	0
18	1.52	2849.99	3	1	175	2
19	1.40	1760.34	3	1	375	1
20	1.33	4217.10	3	1	125	0
21	1.26	54.86	3	1	200	3
22	1.20	657.72	3	1	225	0

23	1.20	2128.52	3	1	225	2
24	1.17	2453.37	3	1	250	3
25	1.15	847.12	3	1	275	1
26	1.03	1458.81	3	1	250	0
27	1.01	2437.85	4	1	250	3
28	1.01	2103.85	3	1	250	2
29	0.97	938.85	3	1	200	0
30	0.96	3133.96	3	1	250	0
31	0.91	1339.71	4	1	275	0
32	0.86	2321.51	3	1	225	1
33	0.83	2298.50	3	1	275	2
34	0.83	1098.58	4	1	250	1
35	0.80	2097.52	3	1	325	1
36	0.80	102.60	3	1	300	0
37	0.73	1320.40	3	1	300	0
38	0.67	1139.87	3	1	325	0
39	0.59	640.53	3	1	225	0
40	0.59	1018.42	3	1	250	0
41	0.57	3712.31	3	1	200	1
42	0.51	3073.21	3	1	75	0
43	0.43	2658.07	2	1	115	0
44	0.42	2073.07	2	1	45	0
45	0.34	2137.68	2	1	40	0
46	0.30	1198.58	3	1	150	1
47	0.30	1086.03	2	1	175	0
48	0.02	3093.21	2	1	20	0

Table 1: Characteristics of the 48 study islands in the Thousand Island Lake, China. Island isolation is given as distance to the nearest mainland.

(2) to cover the minimum area requirement (the smallest island that could maintain a population) of the snakes in the region [23] and (3) to ensure the survey effort on each island was large enough so that all species present could be thoroughly surveyed. Each island was surveyed 30 times, which was sufficient to measure snake richness as demonstrated by the asymptotic behavior of the species accumulation curve [22].

Snake Sampling

We used the line-transect method [25] to determine snake occupancy on the study islands during the breeding seasons between April and July from 2009 to 2013. To facilitate surveys, we cut transect trails (ca. 20 cm wide) that traversed the small islands entirely and the mountain ridges of large islands [22]. To account for the greater habitat diversity associated with larger area (Table 1), the sampling effort was roughly proportional to log (island area) [22,23]. Accordingly, eight transect trails were sampled on island 1 (the largest island, area > 1000 ha), four on islands 2-3 (1000 > area > 100 ha), two on islands 4-6 (100 > area > 10 ha) and one on each of the remaining small islands (area ≈ 1 ha for most islands; Table 1) [23].

Surveys were conducted both in the daytime and in the night because some species are diurnal while others are nocturnal in the region [26]. During the survey, an observer usually walked each transect at a steady pace (ca. 10 m min⁻¹), searching the ground and tree boles with 8×42 binoculars in the daytime (8:00-14:00 h) and with a 12 VDC lamp at night (19:00-24:00 h) [23]. Any snakes detected within 10 m of the transect trails were recorded. All snakes encountered were identified according to [26,27]. A total of 12 snake species were found on the islands (Table 2).

Species	Islands																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
<i>Elaphe carinata</i>	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	0	1	1	0	1	0	1	1	1
<i>Zaocys dhumnades</i>	1	1	1	1	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	0
<i>Bungarus multicinctus</i>	1	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
<i>Rhabdophis tigrinus</i>	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Naja atra</i>	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Trimeresurus stejnegeri</i>	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Deinagkistrodon acutus</i>	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cyclophiops major</i>	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Protobothrops mucrosquamatus</i>	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Oligodon chinensis</i>	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ptyas mucosus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Azemiops feae</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 2: The distribution of snake species on 48 study islands in the Thousand Island Lake, China. Refer to Table 1 for the island codes. Nomenclature follows Zhao (2006).

We used Global Positioning System (GPS) receivers to record the length of each transect (Table 1). Each island was surveyed 30 times, with 15 times in the daytime and 15 times in the night. Surveys were not conducted during inclement weather such as heavy rains or strong winds [22]. To avoid possible systematic sampling bias owing to observer fatigue or weather conditions, the order in which islands were surveyed and the directions in which the trails were walked were randomized and rotated [23].

Ecological Traits

We collected data on four ecological traits for each snake species using field surveys and published literature (Table 3).

Species	Number of islands occupied (n)	Body size (mm)	Clutch size (n)	Geographical range size (km ²)	Population abundance (n)
<i>Elaphe carinata</i>	24	1454.06	8	3302197	12
<i>Zaocys dhumnades</i>	15	1682.91	15	3105264	5
<i>Rhabdophis tigrinus</i>	10	683.07	18	6425370	7

<i>Bungarus multicinctus</i>	7	1130.81	7.5	2458769	4
<i>Cyclophiops major</i>	6	753.19	8.5	3336176	3
<i>Deinagkistrodon acutus</i>	5	1153.1	20	2040812	2
<i>Naja atra</i>	5	1049.44	13	3663270	2
<i>Trimeresurus stejnegeri</i>	3	720.35	6.5	3320817	3
<i>Protobothrops mucrosquamatus</i>	3	852.12	8	2665083	2
<i>Oligodon chinensis</i>	2	598.28	4.5	2018712	2
<i>Ptyas mucosus</i>	1	1201.58	15	3663270	3
<i>Azemiops feae</i>	1	474.50	24	15059900	1

Table 3: Fragmentation vulnerability index (number of islands occupied) and four ecological traits of the snake species inhabiting the study islands in the Thousand Island China, China. Nomenclature follows [27].

We used body length (mm) to represent body size and used clutch size as an index of reproductive potential [9,28]. Following [29], the geographic range size (km²) was obtained from the most recent available published species range maps by digitizing the area into a Geographic Information System (ArcView 10.2). Where no range maps were available, the area of the minimum convex polygon of published point data was calculated excluding areas of water [19]. We used population abundance as a measure of population size for each species [30,12]. Following [8], the population abundance for each species was based on encounter rates during censuses of the largest island (#1; Table 1). The largest (habitat) island can be used as a control site [8,31] because it is more than 1000 ha in size, it has all the snake species (Table 2), and there is no such large-sized site on the neighbouring mainland due to habitat fragmentation. Except for population abundance, all the above data were obtained from [26,27]. For each of the species traits, if a range instead of the mean was given, we used the arithmetic mean of the limits [32,28].

Statistical Analyses

We used the number of islands occupied by each species as the measure of fragmentation vulnerability [9]. This index is regarded as a good predictor of extinction vulnerability [33,7,9] 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 believe the assumption is very likely for the following two reasons. First, the spatial scale of the area is small: the islands were separated by only a few thousand meters within the original continuous mainland [9]. In addition, all study species are common in continuous mainland and would not be expected to have very sparse populations before habitat fragmentation [22].

We used an information-theoretic approach based on Akaike information criterion [34] to assess the associations between the fragmentation vulnerability index and the four ecological traits. We built all possible combinations of models (Table 3). However, interaction effects between ecological traits were not considered because of the limited sample size. We compared model fit and ranked candidate models using the Akaike information criterion corrected for small sample size (AICc). The difference in AICc values between models can be used to calculate Akaike weights (ω_i), which is the probability that the model is the best model in the set of candidate models, given the data [34]. Only models for which $\Delta_i < 2$ are considered to have substantial support [34].

Prior to analyses, we used Shapiro-Wilk test to test whether the response variable and the four ecological traits followed normal probability distributions. We found that the response variable and two independent variables (geographic range size and population abundance) were not normally distributed ($P < 0.05$). Loga-

rithmic transformations were performed on these three variables to normalize values. All analyses were performed using R v.3.3.3 [35].

Results

Fragmentation Vulnerability of Snake Species

Relative vulnerability of snake species to fragmentation as measured by the number of islands occupied varied considerably among species (Table 3). For the 12 snake species included in analysis, the number of islands occupied ranged from 1 (*Ptyas mucosus* and *Azemiops feae*) to 24 (*Elaphe carinata*) (Table 3). That is, *Ptyas mucosus* and *Azemiops feae* were most vulnerable to fragmentation, while *Elaphe carinata* was least vulnerable to fragmentation in our study area.

Ecological correlates of fragmentation vulnerability

For the fragmentation vulnerability index (the number of islands occupied), model selection based on AICc identified population abundance as the best approximating model in the candidate set ($\Delta_i = 0$, $\omega_i = 0.69$) (Table 4).

Model	K	logL	AIC _c	Δ_i	ω_i
1	3	-0.04	9.08	0.00	0.69
12	4	0.48	12.75	3.67	0.11
14	4	0.21	13.29	4.21	0.08
13	4	-0.02	13.76	4.68	0.07
2	3	-3.77	16.53	7.45	0.02
134	5	0.57	18.86	9.78	0.01
124	5	0.55	18.89	9.81	0.01
123	5	0.48	19.04	9.96	0.00
23	4	-3.46	20.63	11.55	0.00
4	3	-5.84	20.69	11.61	0.00
3	3	-6.10	21.20	12.12	0.00
24	4	-3.75	21.21	12.13	0.00
34	4	-5.84	25.40	16.32	0.00
234	5	-3.32	26.64	17.56	0.00
1234	6	0.67	27.46	18.38	0.00

Table: 4 Results of model selection assessing the associations between the fragmentation vulnerability index (number of islands occupied) and a set of candidate models. For each model, number of estimable parameters (K), the log-likelihood (LogL), AIC_c, Akaike differences (Δ_i) and Akaike weights (ω_i) are presented. 1 = Population abundance, 2 = Body size, 3 = Clutch size, 4 = Geographical range size.

The best model suggested that population abundance alone explained 65% of the variance in species vulnerability to fragmentation ($F = 18.532$, $P = 0.002$). The results indicated that snake species with small population size were more vulnerable to fragmentation (Figure 1).

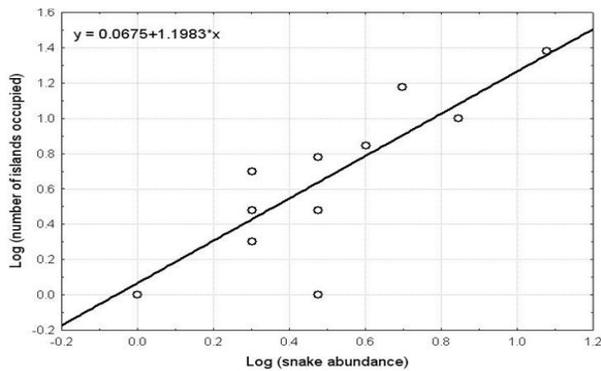


Figure 1: The relationship between the fragmentation vulnerability index (number of islands occupied) and the population abundance of snake species inhabiting the study islands in the Thousand Island lake, China.

In contrast, body size, clutch size, geographic range size and their combinations received considerably less support as predictors of fragmentation vulnerability (all $\Delta_i > 3.67$, Table 4).

Discussion

In this study, we investigated the fragmentation vulnerability of snake species on subtropical land-bridge islands created by the inundation of the Thousand Island Lake, China. To date, existing studies examining the fragmentation vulnerability of vertebrates are extraordinarily biased taxonomically [36]. Among vertebrates, birds and mammals are predominantly studied [10,7,8,12,31,12,28] while few studies have examined snake assemblages [36]. Our study on snakes thus fills in a significant gap, and contributes to the ecological generality of fragmentation vulnerability across a wide range of terrestrial vertebrate taxa.

We found that population abundance was the best single predictor of fragmentation vulnerability for snakes in the Thousand Island Lake. This result supports the hypothesis that species with small population size are more prone to extinction [37,3839]. Considering the short time isolation (ca. 60 years) of our study system, inbreeding, genetic deterioration, demographic and environmental stochasticity may probably be the processes that render small snake populations particularly vulnerable to fragmentation because these processes typically influence populations shortly after fragmentation [18,40,41,42]. Population abundance has also been found to be an important factor influencing the persistence of a variety of taxa in other ecosystems [43,44,30,9,28].

We found considerably less support for body size as a predictor of fragmentation vulnerability. In general, the effect of body size on fragmentation vulnerability is arguable based on current empirical evidence [45,30,8,12,28]. There are at least three reasons that may explain why the relationship between body size and fragmentation sensitivity is equivocal. First, body size is correlated with variables that are themselves positively and negatively correlated with fragmentation vulnerability [15,46]. Moreover, the

relation of body size to several variables (e.g. abundance) seems to change dramatically at different taxonomic levels [47,48]. Finally, although body size is often hypothesized to influence fragmentation vulnerability, it is also linked to dispersal ability [49]. Body size has been shown to be positively correlated with flotation and swimming endurance in reptiles and mammals [50,51]. Thus, large-bodied species may even response positively to habitat fragmentation because they are more mobile [45].

Contrary to our predictions, we found no relationships between fragmentation vulnerability and fecundity or geographical range size. However, previous studies have typically found that species with low fecundity or small geographic ranges are more prone to extinction following fragmentation [17,52,53]. Nevertheless, in our study these two ecological traits did not influence fragmentation vulnerability in snake species. The main reason for the weak relationships is probably that fecundity ($R = -0.173$, $N = 12$, $P = 0.591$) and geographic range size ($R = -0.200$, $N = 12$, $P = 0.533$) are not related to population abundance that largely determines fragmentation vulnerability in snake species.

Our results indicate that population abundance alone explained 65% of the variation in fragmentation vulnerability among the snake species in our study system. Other ecological traits such as population fluctuation, habitat specificity, dispersal ability, annual survival rate, home range size and hunting vulnerability have also been identified as potential factors influencing fragmentation vulnerability in other systems [44,11,54,55]. These traits alone or in combination may account for the remaining variation in species vulnerability to fragmentation in our system. As we currently have no data on these traits, however, these ideas 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 population abundance was the best correlate of fragmentation vulnerability for snakes in our system, while body size, clutch size, geographical range size or their combinations had little or no effects on fragmentation vulnerability. Consequently, snake species with different extinction-proneness traits should be given different conservation priority. As neither large snake species nor those with low fecundity or 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 ecological traits. In contrast, conservation efforts giving priority to species with small population size may prove effective for the preservation of snake species in this system.

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