Rapid morphological change in a small mammal species after habitat fragmentation over the past half-century

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Abstract
Aim: To compare the rapid shifts in body size of mainland and island populations of a native rodent and examine the mechanisms underlying these changes.

Location: Thousand Island Lake, China, which was created in 1959 when the Xin'anjiang Dam was constructed for generating hydroelectricity.

Taxon: The Chinese white-bellied rat, Niviventer confucianus.

Methods: Field surveys were conducted from 2015 to 2018 to collect data on body size of the rodents from a set of islands and nearby mainland sites. We constructed multiple linear models to examine the relationships between body size (length and mass) of rodents and biological variables (predators, competitors and food availability). We also conducted structural equation modelling (SEM) by constructing models via confirmatory path analysis.

Results: All island populations of N. confucianus had significantly larger body size (both body mass and body length) than their mainland counterparts. Moreover, populations on small and more isolated islands had larger body size than their relatives on big islands. The relative absence of predators (large-bodied mammals, snakes and raptors) on islands was most strongly associated with shifts in the body size of rodents. The documented changes occurred after only a half-century of fragmentation.

Main conclusions: The observed rapid body enlargement of rodents after habitat fragmentation is consistent with a release from predation pressure. SEM indicated that island area, rather than island isolation, had positive effects on the abundance of predators, interspecific competitors and food resources, which then had an indirect impact on body size of the rodents. In this study, we report a remarkably rapid case of mammal morphological shifts in a small mammal in response to habitat fragmentation. Given the omnipresence of dams and other anthropogenic disturbances, our findings suggest that a wave of rapid phenotypic shifts in terrestrial vertebrates is taking place in the Anthropocene.
Anthropogenic disturbances, such as land-use change, overexploitation of resources, spread of invasive organisms and climate change, drive contemporary defaunation (Cucchi et al., 2014; Dirzo et al., 2014), which in turn affects ecosystem processes and services and may unleash trophic cascades within ecosystems (Foyle et al., 2005; Hendry et al., 2006, 2017; Young et al., 2016). Land-use change is known to impact biodiversity richness and composition, as well as ecological interactions. For example, large dams, which are built for generating hydroelectricity, have become a visible manifestation of the acceleration of the Anthropocene (Steffen et al., 2015); they frequently inundate landscapes and create archipelagos of land-bridge islands (Jones et al., 2016). These land-bridge islands can be ideal natural laboratories to study the ecological and evolutionary outcomes of habitat fragmentation (Gibson et al., 2013; Wu et al., 2003). For example, anthropogenically driven rapid phenotypic and evolutionary changes, and their ecological mechanisms can be examined in such sites (Hairston et al., 2005; Palumbi, 2001; Stockwell et al., 2003). However, studies focusing on habitat fragmentation, particularly in subtropical regions (Laurance et al., 2014; Malhi et al., 2014), have received less attention.

Animals that can respond quickly to habitat changes by phenotypic plasticity, migration or rapid adaptation have their advantages in a dynamic world dominated by anthropogenic impact. This has been reported in rodents that show changes in several traits (such as total length, tail length and ear length) under conditions of climate change and increased human density (Pergams & Lawler, 2009). Besides, anthropogenic impacts such as biological invasions may accelerate the process of population differentiation, natural selection and adaptive evolution of the invading animals (Colautti & Lau, 2015).

Body size (body mass, body length, etc.) is one of the most fundamental properties of organisms and is associated with many biological traits, such as life history strategy and interspecific competition (White et al., 2007). Documentation of changes in body size provides some examples of rapid evolution of animals (De Amorim et al., 2017; Evans et al., 2012). Some studies have suggested that insular vertebrates often differ strikingly from their mainland specifics (van der Geer, 2020; Lomolino et al., 2013; Millien, 2004). Reduced predation (Steen et al., 1990), reduced interspecific competition (Millien, 2004) and increased intraspecific competition (Adler & Levin, 1994) have been proposed to explain the island rule. Despite over a century of studies conducted by ecologists, evolutionary biologists and biogeographers (Lomolino, 1985, 2005; Lomolino et al., 2012, 2013; Terborgh et al., 2001, 2006), we are far from reaching a consensus on both the generality of patterns (Benitez-Lopez et al., 2021; Köhler et al., 2008; Lomolino, 2005; McClain et al., 2006; Meiri et al., 2008) and the causal mechanisms of evolution in island biotas. In particular, studies that consider the role of biological factors such as predation and competition in body size changes in vertebrates are still needed (Gleditsch & Sperry, 2019; Lomolino et al., 2012). Since the island rule was originally proposed for oceanic islands (from which large predators are often absent), continental islands (which often contain refugium predator populations) are tenuously different because they have been connected to the mainland before they formed. Thus, more studies conducted on land-bridge islands are needed. In summary, there is still much to learn about body size modification in island mammals (especially in continental island mammals), and more comparisons between mainland and island populations are warranted (van der Geer, 2020; Lomolino et al., 2013; Millien, 2004).

Attention to the evolutionary significance of morphological shifts has increased in recent years, and phenotypic plasticity is also more prevalent than previously realized (Donihue et al., 2020). Rapid morphological changes in mammals (Pergams & Ashley, 1999; Rozzi & Lomolino, 2017), birds (Gleditsch & Sperry, 2019; Grant & Grant, 2006; Sendell-Price et al., 2020), reptiles (Stuart et al., 2014), amphibians (Li et al., 2011; Wu et al., 2003) and other animals. In the present study, the observed shifts in body size of the Chinese white-bellied rat Niviventer confucianus were quite rapid (and took only over 50 years) compared with those in similar mammal studies on other mammals. We gathered first-hand data of predators, competitors and food accessibility, instead of simply analysing the effect of island area and isolation on body size variation directly.
et al., 2006) and plants (Biddick et al., 2019) have been reported in recent years. Losos et al. (2004); Losos et al. (2006) have reported numerous cases of rapid morphological and behavioural shifts in lizards, and Schluter (2000) showed that solitary species of sticklebacks exhibit differential morphological features, compared with coexisting species. There is also a broad range of available studies on murids (Adler, 1996; Adler et al., 1994; Pergams et al., 2015; Steen et al., 1990), including introduced murids (van der Geer, 2018, 2020; van der Geer et al., 2018), on islands, that showed rapid morphological changes. The time-scales of the abovementioned studies were usually short, ranging from several decades to centuries on most occasions. Thus, rapid morphological trait shifts in animals are quite possible, even on very short time-scales. Isolated land-bridge islands on which populations that have been isolated from a single common ancestor in the past few decades, however, are relatively rarely used to study rapid phenotypic shifts and its mechanisms.

Mechanistically, several abiotic factors are thought to drive a process of convergence of body size on islands; for instance, island area and isolation are recognized as important abiotic factors affecting the shifts in body size in mammals (Adler, 1996; Lomolino et al., 2013; Meiri et al., 2005). The species–area relationship, in particular, has been described as the closest thing to a rule in ecology; this species–area relationship along with the species–isolation relationship serves as cornerstones that guide our efforts to understand and conserve biological diversity of insular and island-like ecosystems (van der Geer et al., 2016, 2017; Lomolino, 2000; Whittaker & Matthews, 2014). In addition, biotic factors (Lomolino et al., 2012; McClain et al., 2013), such as predators (Michaux et al., 2002; Rozzi, 2018), competitors (Millien, 2004) and food resources (Pergams & Ashley, 1999; Rozzi & Lomolino, 2017), are deemed critical factors leading to phenotypic changes. However, reliable assessment of the direct effect of these biotic forces is frequently difficult to conduct. In addition, it is challenging to differentiate their effects from that of abiotic factors and assess their possible interaction.

The Thousand Island Lake (TIL) is a subtropical land-bridge island system that has been isolated for only about 60 years (Jones et al., 2016; Si et al., 2017; Wang et al., 2015). Rodents are frequently abundant, amenable to monitor and handle and responsive to environmental change in terms of phenotypic traits on both mainland and islands (Pergams & Lawler, 2009). The white-bellied rat (Niviventer confucianus) in our study is one of the most widespread and abundant mammals in the TIL region, allowing for a relatively large enough sample size to be available for study.

Considering all of the above, the selected TIL study system is ideal to examine the following hypotheses: (a) according to the island rule, insular populations of the white-bellied rats (N. confucianus) should have larger body size than their mainland counterparts after isolation; (b) on the basis of ecological release hypothesis, if the insularization of TIL has led to a lack or reduction of predation or competition pressure on most islands we studied, the rodent may have larger food availability and lower allocation of resources to escape predation. Furthermore, rodent populations on islands of different size and isolation may also differ in their body sizes. We examine whether predators, interspecific and intraspecific competitors, and food availability, rather than merely island size or isolation may contribute directly to this phenomenon (Figure 1). These biotic and abiotic factors may have dissimilar effects on body size shifts. We use extensive field data to quantify possible shifts in body size and identify its potential drivers.

2 | MATERIALS AND METHODS

2.1 | Study sites and species

The TIL, China (29°22′–29°50′N, 118°34′–119°15′E), was created in 1959 when the Xin'anjiang Dam was constructed for generating hydroelectricity. The construction of the dam flooded an area of approximately 581 km², which transformed the continuous mountain forest into a heavily fragmented landscape (Figure 2a), creating 1,078 islands, where the area of each island is greater than 2,500 m² when the water is at its highest level (108 m) (Si et al., 2018). Prior to the flooding, the archipelago and the adjacent mainland had similar vegetation, fauna, topography and climate. The major vegetation type of the area is successional forest dominated by the Masson pine (Pinus massoniana) (Yu et al., 2012). The region has subtropical monsoon climate with annual precipitation of 1,430 mm and an average of 155 days of precipitation per year, which is mainly concentrated in the rainy season between April and June. Average annual temperature is 17.0°C, and the daily temperature ranges from −7.6°C in January to 41.8°C in July (Si et al., 2017).

As land-bridge islands, the faunas of the islands and nearby mainland sites have the same origin (Wang et al., 2015). Similar to previous work in human-made Lago Guri, Peru (Terborgh et al., 2006), we sampled mainland sites (n = 4), big islands (area >30.0 ha, n = 7) and small islands (area <10.0 ha, n = 13) due to their representativeness and accessibility (Figure 3). Other islands were not disturbance-free,
or were logistically difficult to monitor, and hence were not considered for sampling.

To get the area and isolation data of the study islands, we digitized the selected islands at 1:5,000 scale using SPOT-6 imagery (website: https://www.intelligence-airbusds.com/en/147-spot-6-7-satellite-imagery). The digitized maps were then rasterized and processed using FRAGSTATS 4.2 (McGarigal et al., 2018). Isolation data (the distance between an island and mainland) were calculated using the Near tool in ArcGIS 10.4 (http://support.esri.com/Products/Desктop/ArcGIS-desktop/arcmap/10-4-1) for a water level of 100 m a.s.l. (Zhao et al., 2020). Characteristics of the 20 selected islands in TIL are listed in Table 1.

Although at least nine rodent species (N. confucianus, N. fulvescens, Apodemus draco, A. agrarius, Leopoldamys edwardsi, Berylmys bowersi, Rattus norvegicus, R. tanezumi and Eothenomys melanogaster) inhabit the study region (Wang et al., 2010), N. confucianus was selected as it is dominant and easy to study due to its high abundance. The rats breed twice a year, and Fagaceae species are the main food source for rodents (Dong, 1989). And the species and sources justifying including them as predators or competitors were listed in Table S1.

2.2 | Data collection

2.2.1 | Rodent surveys

We collected the data on body size by live-trapping rodents along transects from July to September in 2016 and 2017. Sampling effort...
for each island was roughly proportional to its area, resulting in one transect on the small islands and 4 to 8 transects on the big islands and mainland sites (Wang et al., 2010; Zeng & Brown, 1987). On each transect, 10 steel-wired live cage traps (7.5 × 8.75 × 22.5 cm) for small mammals, on which peanuts were placed as baits, were placed at 15-m intervals, and each trap line was sampled for four consecutive nights. Cages were checked early in the mornings to prevent the death of captured animals. Newly captured individuals were identified, marked with distinctively numbered ear tags and released immediately after measurement (Figure 2b). We also recorded sex, body length (measured from nose to rump), body mass, tail length, ear length and foot length of each adult animal before release. We only included adults (the rats with fully erupted third upper molars) in our analyses. The population size on each site was estimated using the mark–recapture method (Zeng & Brown, 1987):

$$N = \frac{M \cdot T}{R},$$

where $N$ is the population size, $M$ is the number of marked rodents initially, $T$ is the total number in the second sample, and $R$ is the number of marked recaptured animals. This allowed us to estimate the population size (density) of $N. confucianus$ and that of its potential competitors.

### 2.2.2 Predator surveys

The primary predators of $N. confucianus$ in the region are snakes, owls and large carnivorous mammals such as wild boars and leopard cats (Dong, 1989). We used the line-transect method to determine snake occupancy and abundance on the study sites. Surveys were conducted both in the day (8:00 a.m.–12:00 p.m.) and in the night (7:00 p.m.–12:00 a.m.) because some species in the TIL region are diurnal and others are nocturnal. Each island was surveyed 15 times (Wang et al., 2012), and the same people conducted these surveys to keep the same detection ability. The order in which sites were surveyed and the direction of trails was walked was randomized to minimize potential biases (Wang et al., 2012).

We surveyed the bird community (with an emphasis on the rodent predators such as $Otus bakkamoena$) on mainland and island sites during 2015–2018. Bird sampling effort on each island

TABLE 1 Characteristics of 20 study islands and 4 mainland sites in the Thousand Island Lake, China. Each site is numbered as in Figure 3

| Site | Area (ha) | Isolation (m) | Island shape index | Habitat richness (n) | Number of transects (n) | Total length of transects (m) |
|------|-----------|---------------|--------------------|----------------------|------------------------|-----------------------------|
| B1   | 1,289.23  | 897.41        | 9.54               | 7                    | 8                      | 3,200                       |
| B2   | 143.19    | 1,415.09      | 4.69               | 6                    | 4                      | 1,600                       |
| B3   | 35.64     | 2,110.41      | 4.01               | 5                    | 2                      | 800                         |
| B4   | 46.37     | 729.80        | 4.46               | 5                    | 2                      | 800                         |
| B5   | 109.03    | 964.97        | 3.77               | 6                    | 4                      | 1,600                       |
| B6   | 55.08     | 953.95        | 3.36               | 5                    | 2                      | 800                         |
| B7   | 32.29     | 1,936.95      | 3.42               | 5                    | 2                      | 800                         |
| S1   | 9.73      | 2,163.77      | 3.41               | 4                    | 2                      | 600                         |
| S2   | 2.83      | 1,238.14      | 1.81               | 4                    | 1                      | 150                         |
| S3   | 1.74      | 2,293.25      | 1.56               | 3                    | 1                      | 300                         |
| S4   | 2.90      | 1,785.30      | 2.33               | 3                    | 1                      | 275                         |
| S5   | 2.29      | 973.85        | 1.51               | 4                    | 1                      | 300                         |
| S6   | 1.01      | 2,103.85      | 1.57               | 3                    | 1                      | 250                         |
| S7   | 0.86      | 2,321.51      | 1.41               | 3                    | 1                      | 225                         |
| S8   | 1.16      | 3,547.09      | 1.13               | 3                    | 1                      | 300                         |
| S9   | 2.23      | 3,261.96      | 2.20               | 3                    | 1                      | 400                         |
| S10  | 1.52      | 849.88        | 1.70               | 3                    | 1                      | 250                         |
| S11  | 2.00      | 1,042.38      | 1.85               | 3                    | 1                      | 300                         |
| S12  | 1.15      | 847.12        | 1.42               | 3                    | 1                      | 275                         |
| S13  | 0.67      | 1,139.87      | 1.72               | 3                    | 1                      | 325                         |
| ML1  | —         | —             | —                  | —                    | 8                      | 8                           |
| ML2  | —         | —             | —                  | —                    | 7                      | 8                           |
| ML3  | —         | —             | —                  | —                    | 9                      | 8                           |
| ML4  | —         | —             | —                  | —                    | 8                      | 8                           |

Note: Area was estimated as the area covered by forest on the islands. Isolation was estimated as the shortest shore-to-shore distance from focal island to the nearest mainland.
was also roughly proportional to the logarithm of the island area. In each survey, observers walked along each transect at a steady pace (approximately 2.0 km/hr) and recorded all the birds that were seen or heard, except the high-flying species passing over the sites. We randomly determined the direction taken by the observer along each transect to limit potential survey biases. Each transect was surveyed nine times every year during our research (Si et al., 2018).

To assess species composition and abundance of carnivore mammals that are predators of rodents, we set camera traps on study islands and mainland sites from 2015 to 2017. The infrared digital cameras (Ltl-5210MC; Ltl Acorn Electronic Co., Ltd) were attached to trees at 40–50 cm above the ground. Cameras faced north or south to avoid triggering caused by sunlight, and vegetation in front of the camera was removed to further minimize false triggering events (Si et al., 2014). Cameras were active 24 hr every day and were programmed to take three photographs after each trigger, and the time interval between each trigger was 15 s. We downloaded the photographs and checked batteries every 2 or 3 months (Zeng et al., 2019).

The abundance and richness of predators and competitors of the focal species was estimated by first making a list of all other mammals, snakes and birds co-occurring on the focal island, and then consulting general references on the diet and habitats of those species, to determine which ones were likely to be significant predators or competitors of *N. confucianus* (Lomolino et al., 2012) (Table S1).

2.2.3 | Food resource surveys

We conducted surveys of all vascular plant species occurring on each mainland and island site during the growing seasons (April–November) in 2017 (Yu et al., 2012). We recorded the richness and abundance of Fabaceae species, which according to *Fauna of Zhejiang Mammalia* (Dong, 1989) are the main food source for rodents within the region. During the surveys, we determined the presence or absence of species through multiple visits to all study sites, following standard field methods designed to record the highest possible number of species. Islands were circumnavigated, and 4–16 transects were established. Number of transects and total length of transects in each of the 20 study islands in TIL are listed in Table 1. We also dissected the stomachs of rodents that had recently died during our field survey. In addition, plants, herbs, seedlings, dead wood, moss, canopy, litter and soil type data were also recorded while conducting this survey.

2.3 | Ethics statement

All aspects of this study were approved by Chun’an Forestry Bureau, TIL National Forest Park and Zhejiang University.

2.4 | Data analyses

2.4.1 | Body size analyses

To determine whether or not males and female rodents both showed increases in body size on islands, we examined male and female *N. confucianus* separately to confirm that both female and male rodents on the islands were larger than their counterparts on the mainland, and individuals of unknown sex were not included in subsequent analyses. To evaluate sexual dimorphism, *t* tests were also performed after removing data that were collected from individuals of unknown sex; the results of the *t* tests were considered non-significant at the *α* = 0.95 confidence level. Thus, data from both sexes were combined in subsequent analyses.

To determine whether island populations of *N. confucianus* differed morphologically from their mainland counterparts, we first compared the mean values of the following variables: body length, body mass, mass/length ratio, ear length and tail length (data from all islands vs. data from mainland sites). To assess the repeatability of shifts across islands, single island comparisons with the mainland were also included. After confirming that all variables were normally distributed by using the Shapiro–Wilks normality test, we used one-tailed, unequal variance *t* tests (Steinberg et al., 2014).

We calculated the standard error of the mean between mainland sites and island sites. Furthermore, we compared standard error of the mean among all mainland sites, big islands and small islands.

Analyses of island parameters, body size parameters of the rodents and the three selective forces were transformed (ln) to meet the requirements for parametric tests.

2.4.2 | Multiple linear regression

To explore the relationship between body size parameters and abiotic factors, we used linear regression models to test the relationships between body length/mass and island area/isolation.

To better understand the complex multivariate biological mechanisms contributing to any rapid morphological shifts in *N. confucianus*, we fit multiple linear models to estimate how the two body size traits of rodents (body length and body mass) responded to the biological variables (predators, competitors and food). We developed a set of candidate models that included all subsets and their interactions. Variable selection and model estimation were based on the Akaike information criterion corrected for small sample (AICc).

2.4.3 | Structural equation modelling

Given the variety of potential factors contributing to the morphological shifts in *N. confucianus*, we also conducted structural equation modelling (SEM) by constructing models via confirmatory path
analysis (Lefcheck, 2016). We specifically utilized piecewiseSEM package, in which paths were built as a set of separate linear equations that were evaluated individually. An original path model was constructed based on our conceptual path diagram (see Figure 1), which was then optimized by removing several non-significant links, starting with the least significant, and continuing stepwise until the shift in AIC associated with one step was less than 2 (Lefcheck, 2016).

All statistical analyses of our data were carried out in R 4.0.1 software (R Development Core Team, 2020).

3 | RESULTS

A total of 537 *N. confucianus* individuals, consisting of 292 females and 245 males, were captured between July 2016 and September 2017. Of these, 106 specimens were captured from mainland sites, 270 specimens from big islands and 161 specimens from small islands.

3.1 | Body size variation

All island populations of *N. confucianus* had significantly larger body lengths and body masses than their mainland counterparts (Table S2; Figure S1). Mean body length of rodents on all islands (139.66 ± 10.26 cm) was 9% larger than that of mainland populations (124.57 ± 12.14 cm), and this difference was statistically significant (t = 9.69, df = 537, p < .001; Figure S2a). Similar observation was made with respect to body mass: a 23% difference (68.03 ± 11.28 g, and 52.70 ± 12.37 g for all island sites and mainland populations, respectively; t = 4.29, df = 431, p < .001; Figure S2b).

Mean body length and mean body mass of rodents from the small islands were slightly but significantly larger than those of rodents from the big islands (body length: 141.61 ± 10.44 cm vs. 138.50 ± 9.99 cm, respectively, t = 4.29, df = 431, p < .001; Figure S2a; body mass: 70.82 ± 11.38 g vs. 66.36 ± 10.90 g, respectively, t = 4.23, df = 431, p < .001; Figure S2b).

When we compared the body size variation between numerous specimens as well as different sites, we observed an increasing trend in both body length and body mass with increasing fragmentation (Figure 4).

Based on the mark-recapture method, the population size was calculated for each island population of *N. confucianus*, the results are listed in Table S2, which showed that bigger population sizes occurred on big islands and mainland sites, while small islands inhabited smaller population sizes.

3.2 | Effects of island area and isolation on body size shifts

We found a significant negative relationship between island area and body mass ($R^2 = .52, p < .001$), and island area and body length of rodents ($R^2 = .40, p = .001$) (Figure 5). However, neither the relationship between island isolation and body mass ($R^2 = .14, p = .06$) nor that between island isolation and body length was significant ($R^2 = .04, p = .20$).

3.3 | Multiple linear models and the role of intraspecific competition

Results of multiple linear models for variation in two body size traits (body length and body mass) of *N. confucianus* in relation to three variables (predators, competitors and food) showed predators had

![Figure 4](image-url) (a) Body mass variation between different sites, and an increasing trend in body mass of *Niviventer confucianus* with increasing fragmentation. Individuals from big island (area >30.0 ha) and small island (area <10.0 ha) populations both have significantly bigger body masses than those from mainland populations ($p < .001$). Dots (in blue colour) illustrate body mass (g) of rodents, notches illustrate median values of body mass, and extreme values are not excluded. (b) Individuals from both big island and small island populations have significantly longer body length than those from mainland populations.
significant effect on both body length and body mass of the rodents (Table S3), while competitors and food did not contribute significantly to the final best-fit model. Predator abundance was the single best model from our selection procedure to explain rat body length ($R^2 = .35, p = .003$) and body mass ($R^2 = .46, p < .001$) shifts across islands (Figure 6).

Population density of *N. confucianus* (intraspecific competition) has a slight significant impact on body size (body length: $R^2 = .13, p = .07$; body mass: $R^2 = .23, p = .02$; Figure S4).

### 3.4 Structural equation models

SEM confirmed that species richness of predators (snakes, owls and large mammals) was the key biological factor that statistically explained the rapid morphological shifts in *N. confucianus* (Figure 7, Figure S5). Further, island area also had a positive effect on the richness of predators, interspecific competitors and the species of Fagaceae family. Isolation was excluded in the final path model (AICc = 168.67), and the ΔAICC value between the best model and the next best model was 16.73. Interspecific and intraspecific competitors had positive but not significant effects on body size shifts on the islands while predators had a negative effect (Figure 7; Table S4).

### 4 Discussion

Our study demonstrated a rapid shift in body size of *N. confucianus* populations that has taken place under anthropogenic habitat fragmentation, following the construction of the Xin’anjiang hydroelectric dam. We found that all island populations of *N. confucianus* had significantly larger body mass as well as body length, than their mainland counterparts, and body size of populations on small islands tended to be larger than those on big islands. Consistent with previous studies (Millien & Damuth, 2004; Pergams & Ashley, 1999), we found that there was no significant sexual dimorphism in body size shifts of *N. confucianus*. Gigantism in rodents has been previously documented in extra-tropical islands (situated at $>27.3^\circ$ latitude) that are small, remote, and lack predators and competitors (Lomolino et al., 2012). In the study sites, the rodents on the land-bridge islands and the mainland had the same origin (Wang et al., 2015). However, after the construction of the dam in 1959, each island became relatively isolated (Table S5).

The current size distribution of rodents on islands seems to be a result of multiple mechanisms (such as genetic adaptation and plasticity) that occurred since isolation, approximately 60 years ago. When populations colonize new habitats, both selection and drift can be experienced due to novel circumstances and founder events (Sendell-Price et al., 2021). Populations that responded quickly to...
habitat changes, whether through evolution or phenotypic plasticity, may have a higher chance of survival in the face of rapid anthropogenic habitat fragmentation. Species surviving in fragmented landscapes are confronted with a modified environment that is characterized by reduced area and increased isolation compared with their larger mainland habitat (Millien, 2006). By showing that selection on small Caribbean islands can simultaneously and independently operate on behaviour and morphology, Lapiedra et al. (2018) also found that rapid environmental changes could simultaneously result in natural selection of multiple phenotypic traits.

The observed body size shifts in *N. confucianus* were very rapid, as have also been reported in other mammals. For example, rapid dwarfing of the feral cattle on Amsterdam Island was observed within 117 years (Rozzi & Lomolino, 2017), whereas the body length of Danish mammals changed within 175 years in response to habitat fragmentation (Schmidt & Jensen, 2003).

In this study, we observed that rodents on big islands had intermediate body size between their mainland and small island counterparts. This is consistent with the principal processes put forward by Lomolino et al. (2012), which suggest that populations on larger and less-isolated islands, with diverse predators and competitors, have less-pronounced divergence from the mainland population. Our findings were consistent with the “island rule,” which was first proposed by Foster (1964); however, the rule has become controversial recently (Meiri et al., 2008), because previous researches have cast doubt on the generality of
this pattern, suggesting that body size changes are asymmetrical (Benítez-López et al., 2021). Indeed, animals on different islands with different areas and degrees of isolation often have various body sizes (Michaux et al., 2002), and the effect of varying areas and isolation also have a disparate impact on ecological interaction. For instance, the greatest effect sizes for ant-plant mutualism interaction types are observed on intermediate-sized islands (Schoener et al., 2016).

In this study, island area showed a negative relationship with the body size of N. confucianus, whereas island isolation had less significant influence on the body size of the rodents. This observation (lack of relationship with isolation) is not consistent with some previous studies that examined the island rule. A probable reason for this inconsistency may be that some studies only found an increase in the number of large-bodied rodents on islands when the isolation distance was more than 10 km (Durst & Ruth, 2015), while the isolation distances measured in our study are comparatively smaller (average value is <2 km). Moreover, the TIL system is actually very different from the oceanic islands that inspired the island rule studies, in which distance from mainland may be more important in explaining body size shifts than it is for land-bridge islands previously connected to the mainland. Consistent with our findings, a study conducted on ants at TIL suggests that island area, not isolation, drives taxonomic, functional and phylogenetic diversity of invertebrates (Zhao et al., 2020). Similarly, Durst and Roth (2012) also found that isolation is not an important factor that influences body size.

The mechanisms underlying the rapid body size shifts of mammals are still not clearly understood (Fietz & Weis-Dootz, 2012; McClain et al., 2013). Many papers have focused on island area or isolation or both, as drivers of body size evolution and other ecological processes (Lomolino et al., 2012; Meiri et al., 2005; Pergams et al., 2015; van der Geer et al., 2016, 2017; Zeng et al., 2019). In this study, we find that island area indirectly affects the shifts in body size; further, rodent body sizes are mediated by biological factors, such as predation, interspecific competition and food resource limitation in different degrees. Among the three biological factors (Table S6), species abundance of predators was the most significant force, and the predation pathway in the SEM exerted a direct negative effect on rodent body size.

Generalist, specialist and mobile (avian) predators are hypothesized to have different effects on rodents, depending on the functional and numerical responses of rodents (Steen et al., 1990). The stabilizing effect of predators on rodent populations depends on factors such as the degree of specialization, mobility, reproductive potential, generation time and the presence of alternative prey (Andersson & Erlinge, 1977). Among all the predators, mammals, reptiles and birds may have a large impact on insular rodents (Michaux et al., 2002). Additionally, some avian species, such as owls, crows and gulls, are considered nomadic specialist predators of rodents (Andersson & Erlinge, 1977). For example, Marström et al. (1988) showed that predation was the dominant factor that synchronized predator productivity with vole abundance. In this study, we also discovered that predation had a considerable statistically significant effect on both body mass and body length of N. confucianus. Thus, the reduced richness of predators (large-bodied mammals, snakes and birds) was a primary factor that influenced the rapid enlargement in body size of N. confucianus on the fragmented islands. This negative association between predator richness and body size has been also documented previously, for example, reduced predator species richness promoted gigantism in a frog species on the Zhoushan ocean islands (Li et al., 2011; Wu et al., 2006). Similar studies conducted on small Caribbean islands have reported differences in morphological shifts (De Amorim et al., 2017), modulation of social signals (Steinberg et al., 2014) and risk-taking behaviour (Lapiedra et al., 2018) in Anolis sagrei lizard populations in the presence or absence of their predator, the Northern curly-tailed lizard (Leiocephalus carinatus). We also found that defaunation of large-bodied mammals (Figure S6) due to habitat loss could release small mammals from top-down control or food resource competition.

In the TIL, due to the absence of rodent predators on islands especially on small islands, the ability of N. confucianus to invest in reproduction may reduce due to ecological release, which makes the rodent...
populations invest more energy on the growth, and thus, the body sizes of island rodents become larger. Thus, it has a greater advantage in the competition with other rodent populations on the islands, leaving the *N. confucianus* individuals have stronger competitiveness. To some extent, the above process (investing more energy on body size growth) can be an evolution of life history of island rodents.

The impacts of interspecific competition and resource limitation on body size shifts were less pronounced than that of predation in our study system. Firstly, interspecific competitors were equally abundant with similar food availability, which were less variable than predator richness, across the mainland and island sites. Secondly, although some studies suggest that resource availability is an important determinant of body size for granivores (Durst & Roth, 2015), we did not observe a significant relationship between food availability and body size in the current study. For example, though there were more *Fagaceae* species (indicating food resource richness) on some islands, and yet rodent body size on these islands was relatively small, whereas some islands with much less food resource richness had some of the biggest *N. confucianus* individuals. This implies that richness and abundance data of *Fagaceae* species may not ideally represent productivity of the island (Cadotte et al., 2008).

Population density and other manifestations such as body mass and reproductive output of the islands syndrome are predicted to increase with degree of island isolation and to decrease with island area, and intraspecific competition favours larger body size of mice (Adler et al., 1994). In our study, population density of *N. confucianus* also has an impact on body size, although the densities of *N. confucianus* in the TIL region are not as high as densities of the rodents in Adler’s study.

Whether the shifts in body size between mainland and island populations of *N. confucianus* resulted from adaptation to altered selective pressures or phenotypic plasticity is an aspect that warrants further research. Common garden experiments are now being performed with lizards (Stuart et al., 2014), ants (Pelini et al., 2012) and other organisms; similarly, rodents raised from embryos in common garden experiments can be used to elucidate this mechanism.

We only studied adult rodents, which have different pelage colours as well as tooth wears (Pergams & Lawler, 2009) compared with juveniles. We also sampled during the same season every year to avoid the effects of gestation on body mass. In the absence of reciprocal transplant experiments, DNA sequencing from each rodent individual, or examining survival and/or reproductive success as a function of body size within study sites could help further determine whether these rapid morphological shifts are a result of evolutionary change or just phenotypic plasticity. However, the type and degree of phenotypic plasticity could also be adaptive and could be a consequence of natural selection and other multiple mechanisms such as founder effects.

To our surprise, we could not find any rodents or their top predators on some small islands even after sampling for two or three years. This suggests that *N. confucianus* was likely extirpated because of the low carrying capacity of these islands, or *N. confucianus* was perhaps never present on these islands. Similar study in Lake Guri, Venezuela reported that small islands lost 75% of their species within 15 years of creation of the dam (Terborgh et al., 2001), whereas Gibson et al. (2013) found that native small mammal communities disappeared rapidly after only 25 years of fragmentation. In fact, some relatively well-established patterns of correlation between body size and extinction risk in mammals create a predictable size-selective defaunation gradient, a pattern that is crucial to understanding global biodiversity loss (Dirzo et al., 2014).

Species and populations that can respond more quickly to habitat changes through phenotypic plasticity or rapid evolution may have survival advantages on habitat islands embedded within human-dominated landscapes. It is essential to understand the potential of such species to rapidly respond to anthropogenic changes, which is crucial for biological conservation. Our findings highlight the importance of considering phenotypic plasticity or even evolution, when developing plans for conservation and management of endangered species that are facing rapid environmental change. We argue that it is critical to establish long-term monitoring programmes as well as international collaborations (Wu et al., 2003) to study modern-day land-bridge islands that could serve as natural laboratories, to understand patterns and processes of phenotypic shifts across terrestrial vertebrate species, which can facilitate efforts for their conservation. As the first documentation of rapid mammal morphological changes after the construction of a Chinese dam, our research may contribute to the understanding of biodiversity conservation in a changing world (Millien, 2006), since many species are being challenged by the accelerated process of fragmentation of natural habitats that characterizes the Anthropocene (Dirzo et al., 2014). Given the omnipresence of habitat fragmentation, our work should be of broad relevance in conservation science and management.

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**CONFLICT OF INTEREST**

The authors have no conflict to declare, and they have no known competing financial interests or personal relationships that could influence the work reported in this paper.

**PEER REVIEW**

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BIOSKETCH
Our research involves a broad range of topics related to island biogeography, habitat fragmentation effects, ecology and conservation biology.

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