

Ecological consequences of the Three Gorges Dam: insularization affects foraging behavior and dynamics of rodent populations

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A number of permanent and seasonal islands will be formed when the world's largest dam, China's Three Gorges Dam, begins to operate at full capacity in 2009. The possible effects of this large-scale habitat insularization on biodiversity and ecosystem processes have attracted considerable attention from scientists around the globe. We investigated the species composition and distribution of rodent populations at two geographic locations in the Three Gorges Reservoir Area through field surveys and determined the dietary composition of dominant rodent species using stable isotope techniques. Our results show that the total rodent density on the islands was significantly higher than that of mainland areas. Stable isotope analysis revealed that the dietary composition of rodents was more diverse on islands than at nearby mainland sites. Moreover, the island populations had greater overlap in food sources than did the mainland populations, suggesting more intense competition for food in the newly insularized habitats. Thus, habitat fragmentation due to the construction of the Three Gorges Dam may substantially increase intra- and interspecific competition among local rodent populations, leading to further changes in species composition and biodiversity.

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After about 18 years of construction, the world's largest dam, the Three Gorges Dam (TGD), has been built on the Yangtze River in southern China, with full operation of hydroelectric facilities expected by 2009 (Wu *et al.* 2004). Water levels have increased by more than 70 m since 2003, when the TGD first began storing water. As a result, some mountains have already become islands, while the area of existing islands in the Three Gorges Reservoir Area (TGRA) has been reduced. Based on studies of land-bridge islands elsewhere (Cosson *et al.* 1999), the reduction in habitat area and the increased isolation of existing habitat in the TGRA may substantially affect the local flora and fauna (Terborgh *et al.* 2001; Wu *et al.* 2003, 2004).

In particular, as habitat on islands increasingly becomes inundated, animals must either migrate uphill or leave the islands altogether. For most ground-dwelling animals, moving upward is the only option. A sudden increase in population density and limitations on space and food may greatly intensify competition within and between species (Wu *et al.* 2003, 2004). Consequently, some animal species may turn to less preferred foods or entirely different food sources from neighboring aquatic ecosystems (Naiman and Décamps 1997; Polis *et al.* 1997; Baxter *et al.* 2005).

To test the above hypotheses, we examined how habi-

tat loss and isolation affect the dietary choices of rodents – important determinants of population dynamics and, thus, species diversity. Specifically, we used field surveys to investigate the species composition and distribution of rodents at two geographic locations in the TGRA, and determined the dietary composition of dominant rodent species based on ¹³C and ¹⁵N stable isotope analysis. Our goal was to take the first step toward assessing possible impacts of the TGD on native biodiversity and ecosystem function by focusing on rodents.

Study area

We chose two islands in the TGRA, Luoqi Island and Huanghua Island, and two contrasting mainland sites as our study areas (Figure 1). Luoqi Island (Site 1; 29° 41' 10" N, 106° 55' 15" E) is located in the upper Yangtze River. This island is about 1.4 km² in area and its highest altitude is 197 m above sea level (asl). Huanghua Island (Site 2; 30° 20' 8" N, 108° 5' 30" E), the largest island in the TGRA, was formed after the construction of the TGD, in 2003; it is 2.3 km² in area and its highest altitude is 248 m asl.

Prior to 2003, during the low-water seasons (from October to April), water levels were about 110 m and 136 m for Huanghua and Luoqi, respectively. After the water level at the dam location rose to 135 m, water levels reached 158 m and 140 m at Luoqi and Huanghua, respectively. The sites that now make up both islands were colonized by humans about 100 years ago and currently support several hundred people. More than 80% of the area of these islands was taken up by agricultural

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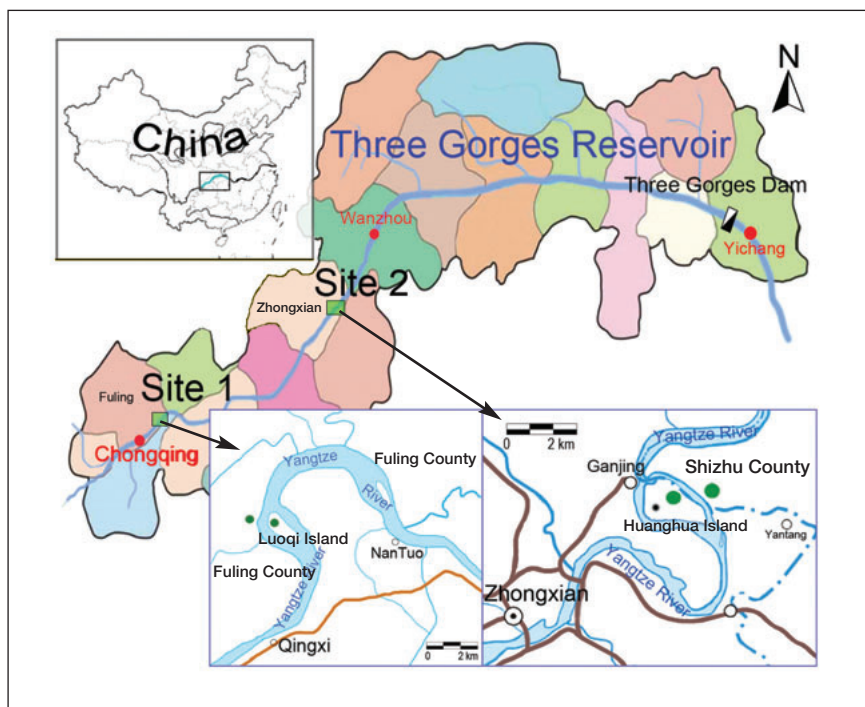


Figure 1. Map of the TGRA, showing locations (solid green circles) of the two pairs of study sites: Luoqi Island (bottom-left inset), Huanghua Island (bottom-right inset), and their adjacent mainland sites.

crops (mainly rice, corn, sweet potatoes, peanuts, soybeans, mung beans, pumpkins, and other vegetables). Also, according to our preliminary survey, the land-use patterns of these islands changed very little as a result of dam construction. A mainland site close to each island, with similar land-use history, human population size, crop types, and total farming area, was chosen for comparison.

Methods

The rodent species at the four study sites were surveyed and measured according to established methods (see WebPanel 1 for details). Tissue samples (blood, muscle, hair) for stable isotope analysis were collected from 3–5 individuals of three dominant rodent species on both Luoqi (ie the Chinese mole shrew [*Anourosorex squamipes*; although taxonomically a member of the Insectivora, we included it in our study], Szechuan vole [*Volemys millicens*], and house rat [*Rattus flavipectus*]) and Huanghua (ie the brown rat [*Rattus norvegicus*], *V. millicens*, and Edward's rat [*Rattus edwardsi*]) over three consecutive nights. These samples were used to evaluate food source shifts at different time scales (week, month, season). Blood samples were drawn from the jugular vein, muscle samples of 1–2 g were excised from the hind leg, and hair samples were sectioned from the distal to proximal end.

There were four potential types of food at our study sites: C_3 non-legumes, C_3 legumes, C_4 plants, and aquatic animals. However, according to gut content analyses made in May of 2005, only two or three types were used

by each rodent species (see WebTable 1). For four of the rodent species in our study, *A. squamipes* mainly consume C_3 non-legumes, C_4 plants, and aquatic animal sources; *R. flavipectus* and *R. edwardsi* feed on C_3 non-legumes, C_3 legumes, and C_4 plants; and *R. norvegicus* eat only C_3 non-legumes and C_4 plants. Thus, the proportion of each food source in rodents' bulk diets can be determined through stable isotope mixing models with either a single stable isotope or two (Peterson and Fry 1987; Phillips and Koch 2002; see WebPanel 1 for details).

We performed all stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) using a Thermo Finnigan MAT Delta^{Plus} XP isotope ratio mass spectrometer coupled with a Flash elemental analyzer (Thermo Finnigan, Bremen, Germany). The measurement precision based on our laboratory standards (urea and glycine), which were calibrated against the International Atomic Energy Agency's standards, was approximately

0.1‰ and 0.3‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

For the rodent capture data, we used a paired *t*-test to detect differences in total density of rodent communities between the islands and the mainland. Two-way analyses of variance (ANOVAs) were used to test the effects of species and habitat on $\delta^{13}C$ and $\delta^{15}N$ values of rodents. For post-hoc testing, we employed the Student-Newman-Keuls (SNK) procedure. We used one-way ANOVAs to test the difference in dietary composition between island and mainland individuals for each species, after the percentage data were arcsine-transformed to satisfy the assumption of homogeneity of variance. Statistical significance for all tests was set at $P < 0.05$. All statistical analyses were performed using SAS (v 8.2), based on the generalized linear model (GLM).

Results

Composition and distribution of rodent populations

The species richness of island and mainland rodent communities was not significantly different at either site, but the dominant species differed significantly between island and mainland habitats (Figure 2). At Luoqi, the three most abundant species occupied different habitats: *A. squamipes* inhabited the river bank, while *V. millicens* and *R. flavipectus* were generally found near the crop fields. At Huanghua, *R. norvegicus*, *V. millicens*, and *R. edwardsi* were the most abundant species on the island, but were found at different elevations. *R. edwardsi* lived

mostly in the lower island region during all three sampling dates, but was also present in the middle island region in May and October 2005; *V millicens* and *R norvegicus* were the dominant species in the middle island regions, while *R norvegicus* was the most dominant species in the upper island region (Table 1). In addition, rodent density was significantly higher in the middle and upper island regions than in the lower island region, when we pooled all data collected at three different times (July 2004, May 2005, and October 2005; one-way ANOVA, followed by paired *t*-test between the lower and upper island region: $t_4 = 2.05$, $P = 0.0571$; and between the lower and middle island region; $t_4 = 2.35$, $P = 0.0321$). The total density of rodents was significantly higher on islands than in adjacent mainland areas (paired *t*-test; Luoqi in May: $t_4 = 5.16$, $P = 0.0067$; Luoqi in October: $t_4 = 3.15$, $P = 0.0345$; Huanghua in May: $t_4 = 4.63$, $P = 0.0098$; Huanghua in October: $t_4 = 3.76$, $P = 0.0197$), and the density of each of the three dominant species increased slightly (but not significantly) in October, at both locations, compared with that in May (Figure 2).

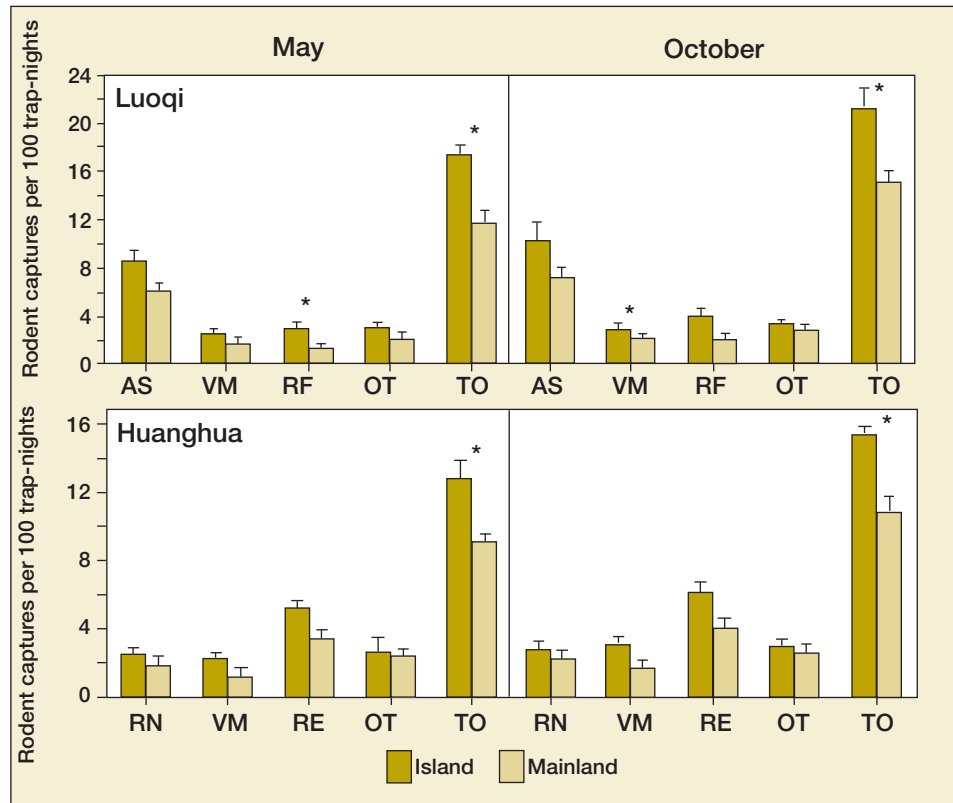


Figure 2. The mean density of each rodent species (the number of rodent captures per 100 trap-nights) in May and October of 2005 at two habitats (island and mainland) of two study locations (Luoqi and Huanghua) in the Three Gorges Reservoir Area (n = 3). AS = *A squamipes*; VM = *V millicens*; RF = *R flavipectus*; RN = *R norvegicus*; RE = *R edwardsi*; OT = other species; TO = total; * = $P < 0.05$.

Isotopic composition of rodents and their potential food sources

The four food sources of rodents (C_3 non-legumes, C_3 legumes, C_4 plants, and aquatic animals) differed in $\delta^{13}C$ and $\delta^{15}N$ values (Figure 3). For the animal tissue samples, we pooled data from tissues and sampling times, because we observed little difference in the $\delta^{15}N$ and $\delta^{13}C$ values among the three tissue types and between the two sampling times. At Luoqi, the $\delta^{13}C$ values of all three dominant rodents on the island site scattered over a similar range (-18‰ to -25‰), while the ranges of $\delta^{15}N$ values differed from each other (Figure 3). There was a significant difference between species in values of

$\delta^{15}N$, but not in $\delta^{13}C$ values at the island site ($\delta^{13}C$: $F_{2,56} = 1.60$, $P = 0.2100$; $\delta^{15}N$: $F_{2,56} = 288.98$, $P = 0.0010$; Table 2). Similar stable isotope distribution patterns were observed

Table 1. The population density and distribution of selected rodent species captured over time at the Huanghua Island site in the Three Gorges Reservoir Area

Species	Density of rodents (captures per 100 trap-nights)								
	Jul 2004			May 2005			Oct 2005		
	L	M	U	L	M	U	L	M	U
<i>Rattus norvegicus</i>	0.6	5.1	6.9	0.0	2.4	5.4	0.0	1.7	6.7
<i>Volemys millicens</i>	1.3	5.9	4.3	0.0	4.2	2.5	0.2	5.1	4.6
<i>Rattus edwardsi</i>	6.8	0.0	0.0	11.3	3.3	0.0	13.5	4.9	0.0
<i>Mus musculus manchou</i>	0.0	3.1	2.5	0.0	1.7	1.8	0.0	2.8	2.5
<i>Apodemus agrarius</i>	1.7	0.7	0.6	0.1	0.7	1.3	0.0	1.4	0.3
<i>Rattus flavipectus</i>	0.5	0.9	0.9	0.2	0.9	0.9	0.2	0.5	0.6
<i>Apodemus sylvaticus</i>	0.7	1.1	0.4	0.0	0.4	0.6	0.0	0.6	0.4
<i>Rattus nitidus</i>	0.0	0.0	0.6	0.0	0.3	0.5	0.0	0.0	0.6
<i>Crociodura attenuata</i>	0.5	0.0	0.0	0.0	0.2	0.1	0.0	0.0	0.0
Total	12.1	16.8	16.2	11.6	14.1	13.1	13.9	17.0	15.7

Notes: L = lower island, <160 m asl; M = middle island, 160–200 m asl; U = upper island, >200 m asl

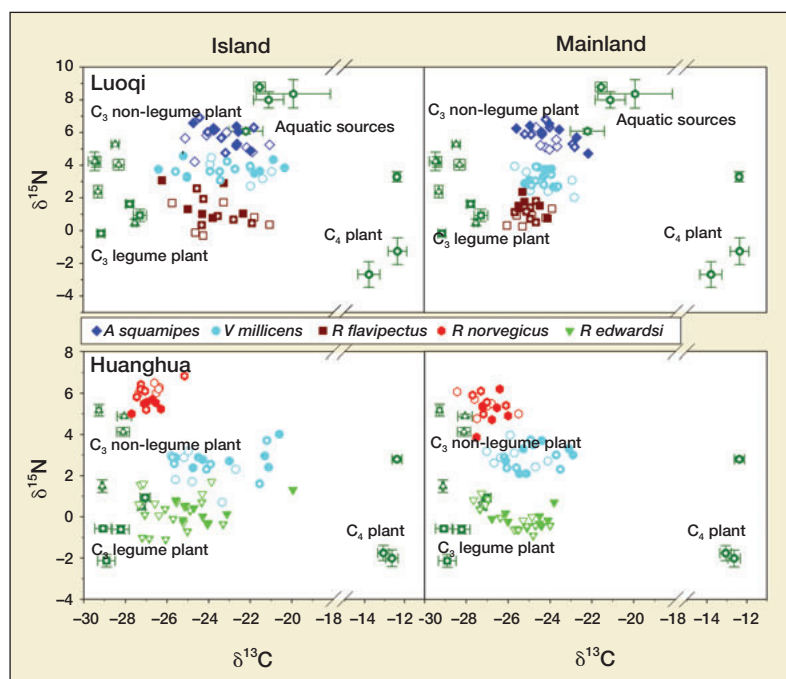


Figure 3. $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ plots for tissue (blood, muscle, and hair) samples from the dominant rodent species and their potential food sources at two habitats of two study locations in the TGRA. The values of each potential food source were given as means ± 1 SE ($n = 5-13$). Dark green symbols represent food source, open symbols represent blood, \square symbols represent muscle, and solid symbols represent hair.

for the rodents at Luoqi's corresponding mainland site, but, for each species, the values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were

Huanghua Island than at the mainland site, while the opposite was observed for *R norvegicus* (Table 3).

Table 2. Mean (± 1 SE) values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from different tissues (blood, muscle, and hair) for each dominant rodent species and their relevant food sources

Location	Species or food source	Island (‰)			Mainland (‰)		
		$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n
Luoqi	<i>A squamipes</i>	-22.6 ^a (0.3)	5.6 ^a (0.2)	18	-23.7 ^a (0.2)	5.8 ^a (0.1)	18
	<i>V millicens</i>	-22.5 ^a (0.4)	3.7 ^b (0.1)	21	-23.8 ^a (0.2)	3.0 ^b (0.2)	21
	<i>R flavipectus</i>	-23.2 ^a (0.4)	1.2 ^c (0.2)	18	-24.6 ^b (0.1)	1.1 ^c (0.1)	18
	C ₃ non-legumes	-28.5 ^a (0.2)	3.7 ^a (0.5)	30	-28.3 ^a (0.3)	3.9 ^a (0.4)	30
	C ₃ legumes	-28.2 ^a (0.4)	0.1 ^a (0.4)	18	-28.1 ^a (0.2)	0.0 ^a (0.3)	18
	C ₄ plants	-12.7 ^a (0.3)	0.0 ^a (1.1)	12	-12.9 ^a (0.2)	0.2 ^a (0.8)	12
	Aquatic sources	-20.4 ^a (0.6)	7.8 ^a (0.8)	24	-21.2 ^a (0.4)	7.9 ^a (0.6)	24
Huanghua	<i>R norvegicus</i>	-26.8 ^c (0.1)	5.9 ^a (0.1)	18	-27.0 ^b (0.2)	5.3 ^a (0.1)	18
	<i>V millicens</i>	-23.9 ^a (0.3)	2.7 ^b (0.2)	24	-25.3 ^a (0.3)	2.8 ^b (0.1)	18
	<i>R edwardsi</i>	-25.2 ^b (0.3)	0.2 ^c (0.1)	30	-25.6 ^a (0.2)	-0.1 ^c (0.1)	24
	C ₃ non-legumes	-28.8 ^a (0.3)	3.9 ^a (0.4)	30	-28.7 ^a (0.3)	3.6 ^a (0.6)	30
	C ₃ legumes	-28.5 ^a (0.4)	0.2 ^a (0.3)	18	-28.2 ^a (0.2)	0.2 ^a (0.2)	18
	C ₄ plants	-12.3 ^a (0.4)	0.3 ^a (0.9)	12	-12.5 ^a (0.3)	0.1 ^a (0.9)	12

Notes: Different superscript letters in rows indicate significant difference among species in a specific habitat ($P < 0.0010$ or 0.0001 ; see text for specific P values). For food source, the same superscript letters indicate no significant difference in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ between two corresponding habitats (islands versus mainland) at each location ($P > 0.05$).

contracted into a smaller range (Figure 3). Significant differences in both $\delta^{13}\text{C}$ values ($F_{2,56} = 11.33, P < 0.0001$) and $\delta^{15}\text{N}$ values ($F_{2,56} = 470.02, P < 0.0001$) were found among species at the mainland counterpart site (Table 2). We calculated the coefficients of variation (CV) in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to determine the variability of food sources among replicate individuals for each dominant rodent species on Luoqi Island and the adjacent mainland site. All CVs for the isotopic values of each rodent species are greater on the island site than on the mainland, except for $\delta^{15}\text{N}$ in *V millicens* (Table 3).

There were also significant differences between rodent species in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at both the Huanghua Island site ($\delta^{13}\text{C}$: $F_{1,71} = 22.07, P < 0.0001$; $\delta^{15}\text{N}$: $F_{1,71} = 373.50, P < 0.0001$) and its mainland counterpart site ($\delta^{13}\text{C}$: $F_{1,71} = 14.37, P < 0.0001$; $\delta^{15}\text{N}$: $F_{1,71} = 497.06, P < 0.0001$; Table 2). The stable isotope composition of *R edwardsi* on Huanghua Island varied greatly, and its $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were spread over a broader range than those of the mainland population (Figure 3). For both *R edwardsi* and *V millicens*, individuals had larger CVs for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values on

Dietary composition and its variation over time

There was no significant seasonal change in dietary composition for any rodent species in either habitat, although we observed some degree of change in the percentage of each food source (Figure 4). At the Luoqi site, *A squamipes* obtained most of its food from C₃ non-legume plants, but C₄ plants and small aquatic animals were also important components of the diet (Figure 4). The percentage of the diet taken from aquatic sources differed between island and mainland habitats (in May: $t_6 = 3.86, P = 0.0071$; in October: $t_6 = 2.61, P = 0.0400$), but this was not the case for the other two food sources. In May, island populations of *R flavipectus* ate significantly fewer C₃ non-legumes ($t_4 = 3.13,$

$P = 0.0352$) and more C_4 plants ($t_4 = 3.59$, $P = 0.0230$) than mainland populations, but there was no significant difference between these groups in C_3 legume consumption (Figure 4). In October, this difference was not significant for any of the three food sources.

At Huanghua, *R. norvegicus* primarily ate C_3 non-legumes, which accounted for more than 90% of its diet at both sampling times. The remaining portion of its food (< 10%) came from C_4 plants (Figure 4). In May, island populations consumed significantly less C_3 non-legume matter, and more C_4 plant matter than mainland populations, but no significant difference was found for either dietary compositions in October. For *R. edwardsi*, differences in food sources (C_3 non-legumes, C_3 legumes, and C_4 plants) between individuals from the two habitats were not detectable for either sampling period, except in October, when island populations consumed substantially less C_3 legume material than did mainland populations ($t_4 = 3.22$, $P = 0.0181$; Figure 4).

Discussion

Islands are generally assumed to support fewer species than those in nearby mainland areas (Lomolino and Weiser 2001; Watson 2002), and to support higher population densities. Our study in the TGRA shows that islands have significantly higher rodent population densities than those in adjacent mainland areas (Figure 2). We propose two explanations for this pattern: (1) a rise in water level drove rodents to higher elevations and reduced the area of non-submerged habitat, and (2) rising water levels decreased emigration to islands. Other possible factors may include higher reproductive success and lower mortality on islands relative to that of the mainland (MacArthur *et al.* 1972; Case 1975). However, Luoqi Island was already a permanent island before the TGD construction, and, like its corresponding mainland site, there was low predation on rodents, because numbers of predators such as snakes and weasels were greatly reduced by intense human activity in the TGRA. We do not have direct evidence to suggest that island populations experience increased reproductive success. In addition, the dominant rodent species varied substantially between Luoqi Island and its mainland counterpart.

The isotope values of animal tissues not only reflect the composition

Table 3. Coefficients of variation (CV, %) in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among the individuals of a specific rodent species at Luoqi Island, Huanghua Island, and their adjacent mainland sites

Species	Island		Mainland	
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Luoqi				
<i>R. flavipectus</i>	6.7	21.3	2.7	12.2
<i>V. millicens</i>	8.3	12.5	3.3	26.0
<i>A. squamipes</i>	5.7	7.3	3.9	6.3
Overall	3.9 ^a	42.1 ^a	2.2 ^b	22.8 ^a
Huanghua				
<i>R. edwardsi</i>	6.5	20.9	4.7	16.4
<i>V. millicens</i>	7.3	12.1	4.7	8.5
<i>R. norvegicus</i>	2.3	5.3	2.7	6.7
Overall	3.0 ^a	137.1 ^a	1.9 ^b	117.4 ^a

Notes: Data from three different tissues and both samplings (May and October) were pooled. Different superscript letters indicate significant differences in CV of $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values between two corresponding habitats (islands versus mainland) at each location ($P < 0.05$).

of the diet, but also provide integrated information on habitat and living conditions (Koch *et al.* 1995; Ben-David *et al.* 1997). According to Tieszen *et al.* (1983), the $\delta^{13}\text{C}$ values of blood, muscle, and hair can reflect the diet of rodents over a time scale of about 1 week, 1 month, and 3 months, respectively. Therefore, the results of our May sampling could indicate food types consumed in

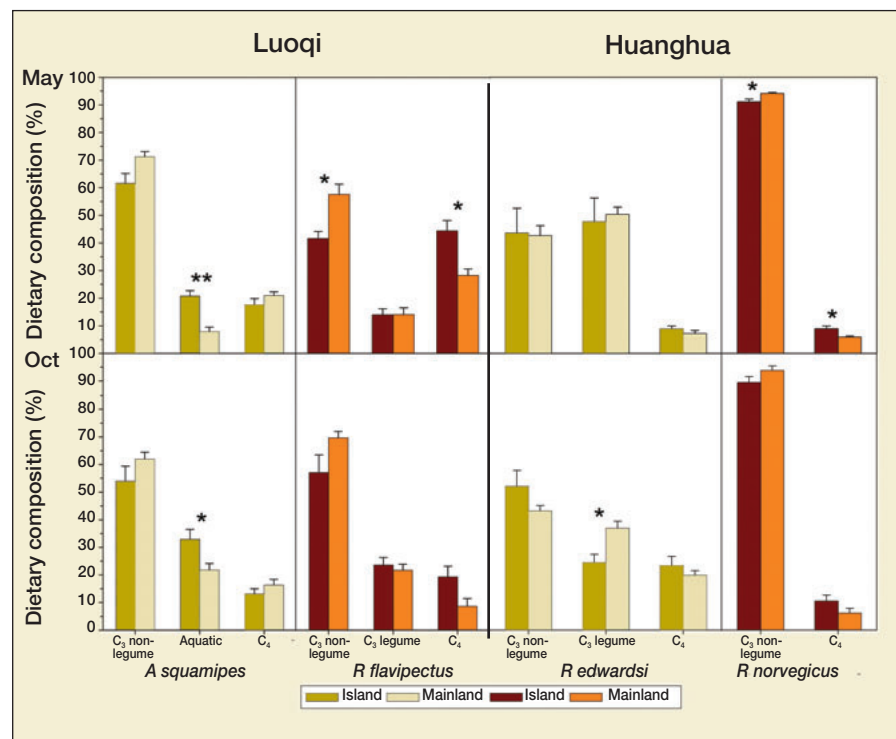


Figure 4. The estimated dietary composition derived from the stable blood isotope ratios for two dominant rodent species at two sampling times and at two sites in the TGRA. * = $P < 0.05$, ** = $P < 0.01$.

February, April, and May, while October sampling could reveal food types consumed in July, September, and October. Thus, the data shown in Figure 3 represent more than 6 months of dietary information on the three dominant rodent species in each habitat. Similar stable isotope compositions imply similar food sources or similar habitat conditions, after correcting for about 3‰ enrichment in $\delta^{15}\text{N}$ and 1‰ or less $\delta^{13}\text{C}$ enrichment associated with each trophic level change (Gannes *et al.* 1998; McCutchan *et al.* 2003; Bearhop *et al.* 2004). The stable isotope signatures of rodent tissues at the mainland site were concentrated to a much smaller range, suggesting that there were abundant food sources, allowing rodents to consume only preferred foods. In contrast, the expanded range of stable isotope signatures observed for island rodents suggests that, within the limited area of the island, multiple species of rodents are forced to compete for the same food sources (Figure 3), given that the food resources and rodent populations are in a state of equilibrium before the rise in the water level. With additional information on the distribution of *R. edwardsi* on Huanghua Island (see Table 1), we hypothesize that the original habitat of this species was at a lower elevation before the TGRA began to store water in 2003. The relatively high variation in its isotopic values suggests that *R. edwardsi* may still be in the process of shifting its diet in response to the construction of the TGD.

On the other hand, the large overlap in stable N isotopic ratios between *R. edwardsi* and *V. millicens* (Figure 3) indicates that *R. edwardsi* has been driven to higher elevations from near-bank locations and now has to compete for space and food with *V. millicens*. In contrast, these two species, and a third species (*R. norvegicus*) on the mainland site of Huanghua, did not overlap in their food sources, as indicated by their distinctly different stable isotope compositions (Figure 3). Thus, both intra- and interspecific competition are expected to be more intense on the newly formed islands than in adjacent mainland areas. This may well be the case for future islands that are formed as the water level continues to rise.

Studies have already revealed that aquatic resources could serve as a complementary food source to fuel high reproduction among rodent populations on islands (Gannes *et al.* 1998; Stapp *et al.* 1999; Stapp and Polis 2003). Our results indicate that *A. squamipes* utilizes aquatic food sources, which may explain why this has become the most abundant species on Luoqi Island. As water levels continue to rise and island area decreases in the near future, the population of *A. squamipes* may have an even greater advantage, as food sources become scarce in early April and late September. In contrast, because the diet of *R. norvegicus* shows selectivity, this species may disappear from Huanghua Island. We found the habitat of *R. edwardsi* to overlap with that of *V. millicens* as populations were

forced to move to higher elevations by rising water levels, so the species' competition for space, food, and other resources will probably intensify.

According to the available data on the land-use history of this region, both the island and mainland sites in this study had experienced similar disturbances as a result of long-term human activities. If the sites were pristine, the findings of rodent density and dietary composition might be different from those presented here. However, such pristine sites do not exist in this region. Other factors, such as differences in food abundance and seasonal shifts in food consumption can also affect stable isotope ratios in the rodents we studied, but these factors were not likely to be important in our study, because the island and adjacent mainland site at each location were so close that they experienced similar climate, crop production, and plant phenology. We also note that, as our study was conducted only one year after the water level rose, rodents might still be adjusting their territories and diets. The differences between island and mainland communities in species composition and food sources may continue to increase over time. Clearly, further research is needed to verify our findings and to compare different animal groups in terms of their responsiveness to habitat loss and fragmentation.

Our results indicate that habitat insularization in the TGRA has affected both the species composition and population dynamics of the local rodent communities. Although little research has focused on other taxa, our findings may be indicative of the fate of other ground-dwelling animals in this region. As one of the first post-dam ecological studies in the area, our study provides important information for assessing possible impacts of the TGD on the species composition and diversity of local animal communities.

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