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ORIGINAL ARTICLE

Small mammal community succession on the beach of Dongting Lake, China after the Three Gorges Project

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Abstract

Although the Three Gorges Project (TGP) may have affected the population structure and distribution of plant and animal communities, few studies have analyzed the effect of this project on small mammal communities. Therefore, the present paper compares the small mammal communities inhabiting the beaches of Dongting Lake using field investigations spanning a 20-year period, both before and after the TGP was implemented. Snap traps were used throughout the census. The results indicate that the TGP caused major changes to the structure of the small mammal community at a lake downstream of the dam. First, species abundance on the beaches increased after the project commenced. The striped field mouse (*Apodemus agrarius*) and the Norway rat (*Rattus norvegicus*), which rarely inhabited the beach before the TGP, became abundant (with marked population growth) once water was impounded by the Three Gorges Reservoir. Second, dominant species concentration indices exhibited a stepwise decline, indicating that the community structure changed from a single dominant species to a more diverse species mix after TGP implementation. Third, the regulation of water discharge release by the TGP might have caused an increase in the species diversity of the animal community on the beaches. A significant difference in diversity indices was obtained before and after the TGP operation. Similarity indices also indicate a gradual increase in species numbers. Hence, a long-term project should be established to monitor the population fluctuations of the Yangtze vole (*Microtus fortis*), the striped field mouse and the Norway rat to safeguard against population outbreaks (similar to the Yangtze vole outbreak in 2007), which could cause crop damage to adjacent farmland, in addition to documenting the succession process of the small mammal community inhabiting the beaches of Dongting Lake.

Key words: beach, Dongting Lake, small mammal community, succession, Three Gorges Project

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INTRODUCTION

Dam construction addresses the relationship between water availability and human needs. Dams have economic and social benefits, such as preventing floods and associated disasters, adjusting water quantity, facilitating agricultural irrigation and generating energy. However, there are also disadvantages to dam construction that negatively impact river basin and reservoir regions. Increasing numbers of scholars have assessed the effects of dam construction on river ecosystems, including water quality control, water and sediment regulation, and biodiversity conservation in downstream areas and reservoirs (Rashad & Ismail 2000; Brismar 2004; Uowolo *et al.* 2005; McCartney 2009; Tullos 2009; Berkun 2010; Dai *et al.* 2010; Zhai *et al.* 2010; Du *et al.* 2011; Lin 2011; Manzini *et al.* 2011; Nazareno & Lovejoy 2011; Qiu 2011; Vaidyanathan 2011; Zhang & Lou 2011; Attwood 2012). China has the richest hydro resources on the planet; hence, the development of hydropower is of great importance to alleviate the energy crisis and environmental pollution resulting from the country's rapid economic growth during the 21st century (Huang & Yan 2009; Chang *et al.* 2010). The Three Gorges Project (TGP) represents 1 of the largest hydropower-complex and flood control projects in the world, and has been the key project for the improvement and development of the Yangtze River. However, the impact of the TGP on the Yangtze River system has been the subject of much controversy since its launch (Fu *et al.* 2010; Zhang & Lou 2011). Many studies have been conducted before and following the construction of the Three Gorges Reservoir (TGR) to determine its actual impact on the surrounding ecosystem (Zheng *et al.* 2002; Jiao *et al.* 2007; Tian *et al.* 2007; Xie & Chen 2008; Yan *et al.* 2008; Liao *et al.* 2010; Yi *et al.* 2010a,b; Zhang *et al.* 2010a,b; Wang *et al.* 2010, 2011, 2012a; Zeng *et al.* 2011). However, there have been limited studies on the small mammal community inhabiting the beaches of Dongting Lake, which is located in the middle reaches of the Yangtze River, downstream of the TGR. Only 1 small mammal study has been conducted to date, focusing on rodents inhabiting the islands of the TGR area (Wang *et al.* 2010). Wang *et al.* (2010) found that the ecological consequences of island formation (insularization) in the TGR area affected rodent foraging behavior and population dynamics. Thus, habitat fragmentation caused by the construction of the TGP might have caused a substantial increase in intraspecific and interspecific competition among local rodent populations, leading to further changes in species composition and biodiversity.

Before the TGP, Dongting Lake had 2270 km^2 of beaches (Liu 1989), which were subject to natural flooding events during the wet season. The region has asymmetrical annual precipitation, with 70%–90% of total annual precipitation occurring during the rainy season, from May to Oct (with the greatest concentration of rain falling between May and Jul). The annual water level of the lake changes by as much as 15 m, rising in summer and falling in winter. Following the commencement of TGR operation in 2003, the flow of the middle and lower reaches of the Yangtze River was altered, which, in turn, changed the exposure time (i.e. period not covered by water) of the beaches of Dongting Lake. Based on the regular pattern of beach emergence periods during the dry season, in parallel to simulated water level data for the lake after the TGR construction, Zou *et al.* (2000a) predicted that the period of low and medium level beach emergence would be significantly lengthened once the TGP was operational. Furthermore, in the mid-term and long-term periods (30 and 50 years) after the completion of the project, the emergence period of the entire beach is expected to gradually lengthen.

In fact, major droughts at Dongting Lake in recent years have been attributed to the changes (Qiu 2011; Ou *et al.* 2012; Sun *et al.* 2012). In comparison to the years before the TGP, lower water levels became a normal phenomenon in Dongting Lake (Lai *et al.* 2012). During the water storage periods of the TGR, the water level decreased by 2.03 m in 2006 and 2.11 m in 2009 at the outlet of the lake, with extreme decreases of up to 3.30 and 3.02 m, respectively (Sun *et al.* 2012). More detailed analyses by Ou *et al.* (2012) generate similar results. These changes in water level inevitably induced alterations to the inundation patterns of the wetlands of this lake, which, in turn, disturbed the ecological function of the lake wetlands as habitats for plant and animal communities, including the small mammal communities. Therefore, analysis of this phenomenon is important (Sun *et al.* 2012). Various studies have been conducted on this topic (plants: Wang *et al.* 2007, Xie & Chen 2008; birds: Wang *et al*. 2012b, Zhao *et al.* 2012; schistosomiasis: Li *et al.* 2007, Zhu *et al.* 2008, 2011, Luo *et al.* 2012; fish: Yi *et al.* 2010a). However, none of these studies have demonstrated the effect of TGR operation on the small mammal communities inhabiting the area surrounding Dongting Lake.

The small mammal communities inhabiting the farmlands surrounding Dongting Lake area may be divided into 2 types, based on dominant species (Chen *et al.* 1988): (i) the Norway rat [*Rattus norvegicus* (Berkenhout, 1769)] and striped field mouse [*Apodemus agrarius* (Pallas, 1771)] pest area and (ii) the Yangtze vole [*Microtus fortis* (Büchner, 1889)] pest area. All 3 species are able to cause major damage to crops, especially during outbreaks (Chen *et al.* 1988, 1998). Furthermore, all 3 species serve as substantial reservoirs of human pathogens. *R. norvegicus* and *A. agrarius* have been extensively studied (Chen *et al.* 1998), because of their dominant species status in the farmlands of this region (Chen *et al.* 1988; Wang *et al.* 2003; Li *et al.* 2005; Zhang *et al.* 2009a). *R. norvegicus* inhabits both fields and buildings, while *A. agrarius* primarily inhabits fields; however, both species were also occasionally caught on the beaches before TGP operation (Chen *et al.* 1998; Li *et al.* 2005). In the second pest area, *M. fortis* primarily inhabits the lake beaches, or nearby rivers, because these areas represent suitable habitats for the voles (Guo *et al.* 1997; Chen *et al.* 1998), which represent the single-most dominant species (Chen *et al.* 1998; Li *et al.* 2005). The vole population has increased rapidly since the 1970s, because of the cultivation of land adjacent to the lake beaches, in addition to soil erosion and the establishment of hydropower stations in the upper reaches of the river (Chen *et al.* 1998; Zou *et al.* 2002). The Yangtze voles migrate between the lake (or river) beaches in the dry season and neighboring rice fields in the summer wet season (Guo *et al.* 1997). In the dry season (from autumn to spring), the beaches serve as the breeding grounds for voles (Wu *et al.* 1996; Chen *et al.* 1998; Zhang *et al.* 2009a). The voles preferentially feed on grasses that grow on the lake beaches (Wu *et al.* 1998). However, in the wet season, when the water level of the lake is high and flooding occurs, the voles retreat to the rice fields, and cause major damage to agricultural crops (Chen *et al.* 1998; Zhang *et al.* 2007a). Damage is particularly severe when the density of the vole population is high and when the lake water level rises rapidly, which is caused by heavy rains or the release of water from upstream hydropower stations along the Yangtze River or other rivers connecting to this watercourse.

Historical data demonstrate that, before the TGP, extensive flooding in summer made the Dongting Lake beaches unstable habitats for small mammal populations other than *M. fortis*. Floods were of longer duration and greater intensity, and appeared to have a greater detrimental impact on the small mammal community (McCarley 1959; Ellis *et al.* 1997; Williams *et al.* 2001). The changes in water level through TGR regulation (Ou *et al.* 2012; Sun *et al.* 2012) have caused the intensity of flooding to decline on the beaches of Dongting Lake during the wet season. Furthermore, it has been hypothesized that water level regulation through the operation of the dam alters the downstream structure and diversity of small mammal communities through changes (an increase or decrease) in habitat size (Anderson & Cooper 2000; Falck *et al.* 2003). Through long-term surveys of small mammals inhabiting the beaches of Dongting Lake, we observed changes in the structure of the small mammal community. Hence, in the current study, we aim to compare the abundance of species in the small mammal community inhabiting the beaches of Dongting Lake before and after the TGP operation, and to examine how the community structure and species composition have changed across 4 sampling periods that reflect different TGR water impoundment levels. We hypothesize that the increase in beach exposure time after the TGP has caused some species inhabiting farmland areas to shift/expand their habitat range to beaches that were previously uninhabitable, because of seasonally high inundation levels. In other words, we investigate whether the regulation of water has caused the small mammal communities to relocate to the beaches. This hypothesis assumes that small mammals in this region are strongly affected by flooding, and that they benefit from the reduced intensity (extent and duration) of inundation following water regulation by the operation of the TGP dam.

MATERIALS AND METHODS

Study site

The Dongting Lake region is located in the middle reaches of the Yangtze Valley, downstream of the TGR, in the northern part of Hunan, China (28°30′–30°20′N and 111°40′–113°10′E). It is in a subtropical region that has 4 distinct seasons. The weather is warm and humid, with a mean annual temperature of 16–17 °C, and mean annual rainfall ranging from 1200 to 1550 mm. It is one of the most important regions for agricultural production in the Yangtze Valley region of China.

The survey sites were scattered along the beaches of Dongting Lake (Fig. 1), mainly including the beaches in the vicinity of Matang Polder (29°14.5′N, 113°03.2′E) in Yueyan County, Beizhuzhi Township, Datonghu County (29°10.1′N, 112°47.7′E) and Nandashan Polder (29°4.1′N, 112°48.2′E) and Chuangye Polder (28°59.6′N, 112°15.1′E) in Yuanjiang County. The TGR began storing water in 2003; hence, the 1990s field surveys represented the small mammal community status before TGR regulation. However, continuous surveys were only conducted on the beaches near Matang Polder in the 1990s. Therefore, to obtain a comprehensive overview of the situation, we included all fragmen-

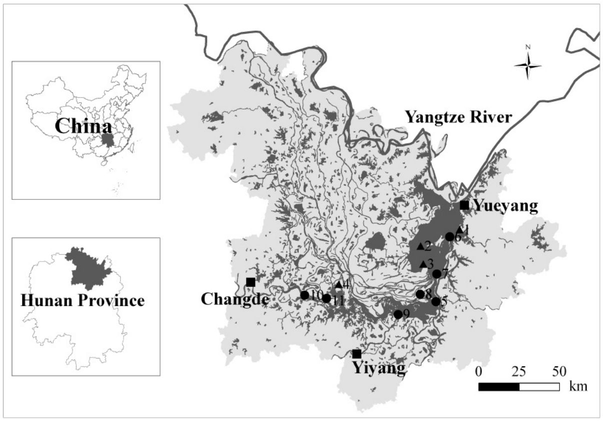

Figure 1 Sampling sites in the Dongting Lake region. The sampling sites including regular surveys points (showed by ▲): the beaches in the vicinity of (1) Matang Polder in Yueyan County; (2) Beizhuzhi Township, Datonghu County; (3) Nandashan Polder; and (4) Chuangye Polder in Yuanjiang County. Fragmentary survey points (shown by ●): the beaches in the vicinity of (5) Quyuan Farm in Miluo County; (6) Lujiao in Yueyan County; (7) Luhu and (8) Chapanzhou in Yuangjiang County; (9) Liujiahu in Yiyan; (10) Hejiashan Farm in Changde; and (11) Potou in Hanshou County.

tary surveys from additional sites other than this survey location, including the beaches outside of Quyuan Farm in Miluo County (28°51.4′N, 112°51.9′E), Lujiao in Yueyan County (29°12.4′N, 112°59.2′E), Luhu (29°0.5′N, 112°53.1′E) and Chapanzhou (28°54.2′N, 112°46.1′E) in Yuangjiang County, Liujiahu in Yiyan (28°48.1′N, 112°37.0′E), Hejiashan Farm in Changde (28°56.8′N, 112°1.7′E) and Potou in Hanshou County (28°55.2′N, 112°10.6′E). All survey areas fell within the alluvial plain (catchment area) region of Dongting Lake, and are at an altitude of approximately 25–30 m asl. All survey areas were covered by water during the flooding season (approximately 3–5 months, almost from May to Oct) in normal years. Dikes (levees) were positioned around the lake, separating the survey beaches from the adjacent farmland to protect the local residents and their farmland and houses from flooding. There were no agricultural activities on the beaches. In the 1990s, the vegetation on the beaches was dominated by *Carex* spp., *Phragmites* spp., *Triarrherca* spp. and *Polygonum hydropiper*. From the early 2000s, the forested area expanded rapidly, particularly *Populus* spp. (mainly *Polygonum deltoids* and *Polygonum euramevicana*), which paralleled increases in beach exposure time (Xie & Chen 2008; Hou *et al.* 2011) and the implementation of a project to restore lake habitats converted from farmland in the Dongting Lake region (Zhang *et al.* 2009b).

Methods

Snap traps (150 × 80 mm, Guixi Mousing Tool Factory, Jiangxi, China) were used throughout the 20-year survey period. Snap traps were selected to study the small mammal communities in this area (Chen *et al.* 1988, 1998), as all species could be effectively captured using this technique. Trapping sessions (each lasting a single night) were carried out 3 times a year, in spring (mainly in Apr or Mar), autumn (mainly in Oct or Sep) and winter (mainly in Jan or Dec), except when surveys were fragmentary during the period of 1997–1999. Surveys were not conducted in summer, because of the beaches being submerged during the wet season. Traps were baited with fresh sunflower seeds, and then placed on the ground in the afternoon, and collected the next morning. Three or 4 plots of approximately 6–10 ha each were sampled along a line transect. A total of 80–100 traps were set in each plot (approximately 200–300 traps for each treatment). On the beach outside of Matang Polder, the survey plots were located approximately 1000–2500 m away from a dike; 1 line transect was parallel to the dike (approximately 1000 m from the dike), while the other line transects were perpendicular to the dike (approximately 1500–2000 m from the dike). On the beach outside of Beizhuzhi Township, the survey plots were located approximately 6000–8000 m from a dike, with all line transects positioned perpendicular to the dike. On the beach outside of Chuangye Polder, the survey plots were located approximately 1500–2000 m from the dike, with all line transects being perpendicular to the dike. On the beach outside of Nandashan Polder, 2 survey plots were located approximately 1000–1500 m from a dike, and line transects were parallel to the dike; the other 2 line transects were located in a perpendicular direction approximately 2000–2500 m from the dike. The other fragmentary surveys sites were located approximately 2000–5000 m from the dikes, and all were oriented in a perpendicular direction from the dikes. Because of the repopulation of small mammals on the beaches after flooding, traps were consistently set in the same plots. Traps were spaced approximately 5 m apart. Captured animals were transferred to the laboratory and identified.

Analysis

Water storage (impoundment) was initiated at the TGR in a stepwise fashion from 135 m asl in late 2003, to 156 and 172 m asl in late 2006 and late 2008, respectively (Fu *et al.* 2010). From 2008 to 2012, experimental storage up to a final water level of 175 m asl was conducted annually. Therefore, the evaluation of the small mammal communities was divided into 4 periods, based on the stage of water storage: (i) before construction in the 1990s (1992–1994, and fragmentary surveys in 1997–1999); (ii) the first partial filling period (2003–2006); (iii) the second partial filling period (2007–2008); and (iv) during experimental water storage to a final water level of 175 m (2009–2012). Data from each period were pooled for the analysis of community structure, because of the low number of captured individuals of some species, to overcome the issue of occasional surveys in each single investigation, and to smooth the influence of strong oscillations of *M. fortis* (Zhang *et al.* 2010b). Only 1 sampling site was continuously surveyed in the 1990s (the beach outside of Matang Polder); hence, fragmentary surveys from other locations were pooled with this dataset to provide an overview of the situation before the TGP, allowing overall trap success to be calculated for all nights during which traps were set in each period.

Relative population abundance was indicated by trap success, and calculated as the percentage of success in 100 traps: $D = (100N / T) \times 100\%$, where D is the relative population abundance, N is the number of animals caught by all traps, and T is all traps collected the next morning.

The dominant concentration index (C) and degree of dominance (I) were calculated using the methods described by Simpson (1949): $C = \sum (Ni/N)^2$, $I = Ni / N$, where Ni is the number of animals per species and N is the number of animals.

The Shannon–Weiner diversity index (H′) was calculated using the equation (Shannon & Wiener 1949) $H' = -\sum_{i=1}^{s} Pi \ln Pi$, where S is the number of species; $Pi = Ni / N$, where N_i is the number of species i and N is the number of animals.

The evenness index was calculated following Pielou (1966): $E = H' / lnS$.

Similarity coefficients (S_1 and S_2) of the small mammal community were calculated based on the Sorenson index: $S = 2c / (a + b)$, where, for S_1, a and b represent the number of rodent species of the 2 communities, and c represents the total number of mutual species in the 2 communities. For S_2, a and b represent the total rodent density (trap success per 100 traps) of the 2 communities, and c represents the total least density of mutual species in the 2 communities. S_3 is the similarity coefficient of percentage based on the Whittaker index: $S_3 = 1 - 0.5\ (\sum|a_i - b_i|)$, where a_i is the ratio of species i in community a, and b_i is the ratio of species i in community b.

The significance of differences in species composition for the 4 successive periods was determined using Fisher's exact test. The t-test of the Shannon–Weiner index followed the method of Hutcheson (1970):

$$t = \frac{Hi' - Hj'}{\sqrt{Var(Hi') + Var(Hj')}} \ ,$$

where Hi' and Hj' are the Shannon–Weiner diversity indices of communities i and j; and Var(Hi') and Var(Hj') are the estimates of their variance, which were calculated using:

$$Var(H') = \frac{\sum Pi(\ln Pi)^2 - (\sum Pi \ln Pi)^2}{N} + \frac{S-1}{2N^2} \ ,$$

where $Pi = Ni / N$, N_i is the number of species i, N is the number of animals and S is the number of species.

Finally, the degree of freedom (df) was calculated by:

$$\mathrm{df} = \frac{[Var(Hi') + Var(Hj')]^2}{[Var(Hi')]^2/Ni + [Var(Hj')]^2/Nj} \ .$$

RESULTS

Species composition of small mammals on the beaches

In total, 31 812 traps were set and 3262 animals were caught (excluding 95 traps that contained the remains of animals that escaped, such as tails, claws, bloodstains and hair) between 1992 and 2012 on the beaches of Dongting Lake (Table 1). *M. fortis* was the dominant beach species (74.00% species composition), followed by *A. agrarius*, *R. norvegicus*, the house shrew [*Suncus murinus* (Linnaeus, 1766)] and the harvest mouse [*Micromys minutus* (Pallas, 1771)] (22.40%, 2.05%, 1.10% and 0.25% species composition, respectively). All other species were only caught occasionally; these species included the chestnut white-bellied rat [*Niviventer fulvescens* (Gray, 1847)] (0.06% species composition), the Himalayan rat [*Rattus nitidus* (Hodgson, 1845)] (0.03%) and the hedgehog [*Erinaceus europaeus* (Linnaeus, 1758)] (0.03%). Differences in species composition were visible before and after the commencement of TGP operation. For example, *A. agrarius* and *R. norvegicus* rarely inhabited the beach prior to TGR operation, but were universally captured after 2003. In addition, the species composition ratio of these 2 species steadi-

Table 1 Species composition of the small mammal community from 1992 to 2012 on the beaches of Dongting Lake

Period	Trap number	Number of captured animals†	Species composition (%)‡							
			Microtus fortis	*Apodemus agrarius*	*Rattus norvegicus*	*Micromys minutus*	*Niviventer fulvescens*	*Rattus nitidus*	*Suncus murinus*	*Erinaceus europaeus*
1990s	4682	624	99.68 (622)	0.00	0.16 (1)	0.16 (1)	0.00	0.00	0.00	0.00
2003–2006	5561	384 + 12	81.77 (314)	15.89 (61)	0.52 (2)	0.00	0.00	0.00	1.82 (7)	0.00
2007–2008	8410	1158 + 47	79.36 (919)	17.70 (205)	1.47 (17)	0.17 (2)	0.09 (1)	0.00	1.12 (13)	0.09 (1)
2009–2012	13159	1096 + 36	51.00 (559)	42.61 (467)	4.29 (47)	0.46 (5)	0.09 (1)	0.09 (1)	1.46 (16)	0.00
Total	31812	3262 + 95	74.00 (2414)	22.47 (733)	2.05 (67)	0.25 (8)	0.06 (2)	0.03(1)	1.10 (36)	0.03 (1)

†The numbers following '+' are the remains of escaped animals found in traps, such as tails, claws, bloodstains and hair. ‡The numbers in parenthesis are the animals of each species that were trapped.

ly rose across the 20-year survey period. The 1990s species composition data for the beaches (Table 1) clearly show that TGR water regulation in subsequent years had a major influence on the structure of the small mammal community inhabiting the beaches. Fisher's exact test for species composition indicates that there was a significant difference in species composition among periods (df = 21, $\chi^2 = 662.377$, $P < 0.001$; Table 2), with χ^2 values becoming increasingly larger; however, there was no difference between the 2003–2006 and 2007–2008 periods.

Relative population abundance of small mammal species

Fluctuation in the relative population abundance (total trap success) of *M. fortis* among the 4 periods before and after TGR impoundment was recorded (Fig. 2). Because vole numbers peaked during the 1990s and 2007–2008, more individuals were captured during these years compared to 2003–2006 and 2009–2012. Furthermore, evaluation of *A. agrarius* and *R. norvegicus* ratios indicated continued population growth throughout the study period (Fig. 2). According to the statistics for all data years combined (including data from the spring, autumn and winter of each year), there was a noticeable rise in *A. agrarius* and *R. norvegicus* population abundance from the 1990s to 2012 (Fig. 3). *A. agrarius* exhibited the greatest population growth of all recorded species, after shifting to the exposed beach habitats. For instance, *A. agrarius* individuals were not caught on the beaches during the 1990s, yet by 2009–2012 trap success was very high (3.5%), particularly in Jan and Apr of 2012 (trap success: 6.5% and 5.8%, respectively).

The dominance index and the index of dominant concentration

Based on the dominant concentration index (Simpson index), TGR operation altered the small mammal community, by reducing the prominence of certain dominant species and increasing community diversity (Table 3). With succession, the Simpson indices for the beaches (*C*-value) also declined in a stepwise fashion.

Diversity index and evenness of small mammal communities

The species abundance of the small mammal community was higher on the beaches of Dongting Lake after the commencement of TGP operation. In the 1990s, only 3 species were caught on the beaches (*M. fortis*, *R.*

Table 2 Fisher's exact tests of species composition among the 4 census periods

		Degree of freedom			
		1990s	2003–2006	2007–2008	2009–2012
X^2	1990s	—	4	6	6
	2003–2006	141.562***	—	6	6
	2007–2008	207.249***	4.990	—	7
	2009–2012	591.301***	127.075***	209.596***	—

***$P < 0.001$.

Table 3 The dominance index (*I*) and the index of dominant concentration (*C*) for small mammal communities before and after the Three Gorges Reservoir operation

Index	Species	Period			
		1990s	2003–2006	2007–2008	2009–2012
I-value	*Microtus fortis*	0.9968	0.8177	0.7936	0.5100
	Apodemus agrarius		0.1589	0.1770	0.4261
	Rattus norvegicus	0.0016	0.0052	0.0147	0.0429
	Micromys minutes	0.0016		0.0017	0.0046
	Niviventer fulvescens			0.0009	0.0009
	Rattus nitidus				0.0009
	Suncus murinus		0.0182	0.0112	0.0146
	Erinaceus europaeus			0.0009	
C-value		0.9936	0.6942	0.6615	0.4438

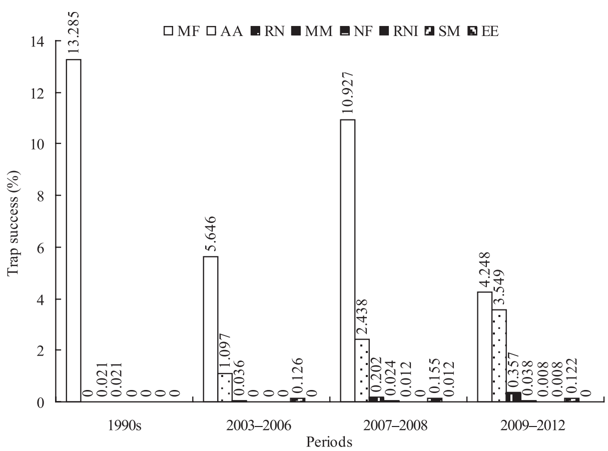

Figure 2 Trap capture success of small mammal community species for each census period. MF, *Microtus fortis*; AA, *Apodemus agrarius*; RN, *Rattus norvegicus*; MM, *Micromys minutus*; NF, *Niviventer fulvescens*; RNI, *Rattus nitidus*; SM, *Suncus murinus*; EE, *Erinaceus europaeus*.

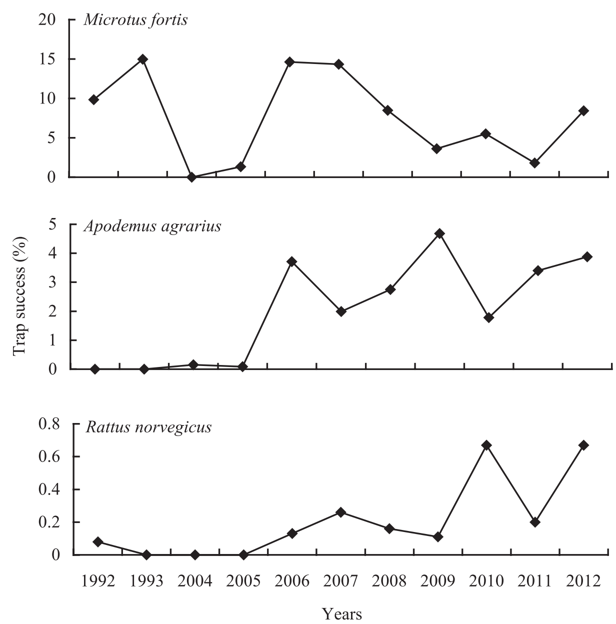

Figure 3 Trap capture success of *Microtus fortis*, *Apodemus agrarius* and *Rattus norvegicus* for all survey years that had data for 3 seasons (spring, autumn and winter) in a given year.

norvegicus and *M. minutes* [Table 4]). After water storage was initiated in 2003, 4 species were caught on the beaches, with *A. agrarius* being caught during the first impoundment period. Then, during the second (2007–2008) and third (2009–2012) impoundment periods, the number of species caught on the beaches rose to 7. A similar trend was recorded for the species diversity index *H′* (Shannon–Weiner index) and the evenness index *E* (Pielou index) before and after the commencement of TGR operation. Initially, in the 1990s, low Shannon–Weiner and Pielou indices were recorded for the small mammal community. These values rose after the commencement of the TGR operation, when the TGR began to impound water (Table 4). The *t*-test showed noticeable changes in the small mammal community on the beaches of Dongting Lake; the difference among different periods was significant, except between 2003–2006 and 2007–2008 (Table 5). Furthermore, the *t*-value became greater when comparing the 1990s data with each of the subsequent 3 periods following the commencement of TGR water impoundment (i.e. from the first impoundment period [2003–2006] to the highest level of water storage at 175 m [2009–2012]). In other words, the significant difference became larger with each subsequent period (Table 5).

Similarity index of the 4 census periods

The similarity index S_1 showed that the small mammal community became increasingly similar during the periods after TGR operation (Table 6); however, simi-

Table 4 The diversity index (*H′*) and evenness (*E*) before and after Three Gorges Reservoir operation

Index	Period			
	1990s	2003–2006	2007–2008	2009–2012
S	3	4	7	7
H’	0.0238	0.5572	0.6255	0.9410
E	0.0217	0.4019	0.3214	0.4836

Table 5 Statistical analysis (*t*-test) of the species diversity index (*H′*) among different census periods

		Degree of freedom			
		1990s	2003–2006	2007–2008	2009–2012
t-value	1990s	—	475	1676	1684
	2003–2006	11.81***	—	707	615
	2007–2008	19.73***	1.36	—	2214
	2009–2012	33.91***	7.93***	8.99***	—

***$P < 0.001$.

Table 6 Similarity index among different census periods

	Period	1990s	2003–2006	2007–2008
S_1	2003–2006	0.5712	—	
	2007–2008	0.6000	0.7273	—
	2009–2012	0.6000	0.7273	0.8571
S_2	2003–2006	0.5543		
	2007–2008	0.7933	0.6439	
	2009–2012	0.3913	0.6999	0.6141
S_3	2003–2006	0.8193	—	—
	2007–2008	0.7968	0.9689	—
	2009–2012	0.5132	0.6887	0.7156

larity before and after the commencement of dam operations was low. Because S_1 was based on the number of species in the community alone, this parameter may indicate that some species began to use the beaches soon after the TGR began to operate and impound water. Because the similarity coefficient S_2 was calculated from both the community structure and the density of each species in the community, S_2 always remained relatively low, except for the higher index obtained between the 1990s and 2007–2008, which reflected the higher densities of *M. fortis* in these 2 periods compared to the other periods. S_2 also indicated an increase in the density of species migrating to the beaches. An equivalent tendency was found in S_3, with the S_3 similarity coefficient of the 1990s and 2009–2012 being lowest. S_3 was based on the community structure of species and on the species composition of the community; hence, the high ratio of *M. fortis* and *A. agrarius* contributed to a larger value of S_3 compared to S_2. In any case, the values of S_1, S_2 and S_3 between the 1990s and 2009–2012 were almost consistently the lowest.

DISCUSSION

Although most of the world's river systems are regulated by humans to some extent, information about the effects of river regulation on mammals remains limited. In fact, speculation about how river regulation affects mammal communities is more common than actual empirical data (Nilsson & Dynesius 1994). This paper presents 1 case of how a dam, the TGP, affects a small mammal community inhabiting the beaches of Dongting Lake, downstream of the dam. The TGP represents 1 of the world's largest hydraulic projects and, as such, has been the subject of much controversy. After decades of planning, and 17 years of construction, the project has demonstrated comprehensive benefits with respect to various issues, including flood control, power generation and navigation. In parallel, various environmental and ecological issues have begun to emerge following the commencement of TGR operation, particularly when operating at full capacity (Dai *et al.* 2010; Fu *et al.* 2010). However, debate about the drawbacks of dam use continue, including pollution, silt accumulation, ecological deterioration, and the geological hazards of reservoirs created by dams, or the upstream/downstream sections of rivers immediately adjacent to dams. Limited research has been conducted regarding how dams impact the ecology of lakes downstream. Nevertheless, the TGR might be associated with the population outbreaks of *M. fortis* in 2007 (Zhang *et al.* 2007a, 2012a) and with the rare drought recorded at Dongting Lake in 2011 (Qiu 2011). Although the TGR was probably not the sole cause of these issues, it almost certainly exacerbated the situation. According to the results presented in the current study, out of the 8 species captured on the beaches after commencement of TGR operation, only 3 (*M. fortis*, *R. norvegicus* and *M. minutus*) were recorded inhabiting the beaches during the 1990s. It is possible that the other species were also present during the dry season, but were not captured because of only a small number of individuals being present. In particular, the *R. norvegicus* and *A. agrarius* populations showed a noticeably increasing trend in abundance (Figs 2 and 3) after the commencement of TGP operation. Hence, changes in the structure of the small mammal community at Dongting Lake present a clear example of how this dam has impacted the natural ecology of the region; therefore, ecological impact assessments should take into account the impact of the TGP on downstream lakes.

Among the 3 dominant species (*M. fortis*, *A. agrarius* and *R. norvegicus*) inhabiting the beaches after the commencement of the TGR operation, *M. fortis* was the only confirmed dominant species originally inhabiting the beaches (Chen *et al.* 1998; Li *et al.* 2005). The life-history of this species is closely related to seasonal changes in the exposure of the beaches at Dongting Lake (Chen *et al.* 1998; Wang *et al.* 2004; Li *et al.* 2005). *M. fortis* has been a focus species in the small mammal community of Dongting Lake because of the major damage that this species causes to agriculture, and its relationship with the beach. A detailed impact assessment of the effect of different TGR water impoundment levels on *M. fortis* was undertaken prior to dam construction (Zou *et al.* 2000a,b, 2002). The analysis of historical records and long-term trapping studies revealed that fluctuations in the vole population in the Dongting Lake region were largely determined by the timing and duration of the availability of their preferred habitat; namely, the lake beaches. In turn, the size of the vole populations on the beaches prior to flooding determined the magnitude of their effects on neighboring agricultural crops. Hence, an increase in the beach area of this region over the past 100 years has probably contributed to the growth of the vole population, and, consequently, increasing damage to nearby agricultural crops (Chen *et al.* 1998). It was predicted that the regulation of water flow by the TGR might reduce water levels in autumn, thus increasing the amount of time that voles had access to preferred beach habitats, which would, consequently, result in larger vole populations and greater damage to surrounding crops (Zou *et al.* 2000a,b, 2002). The outbreak of the vole population in the Dongting Lake region during 2007 seemed to reasonably support this forecast (Zhang *et al.* 2007a). Despite this, the ratio of voles in the overall species compositions has declined compared to before dam operation, because of the immigration of other species to the beaches, particularly *A. agrarius* and *R. norvegicus*.

Apodemus agrarius and *R. norvegicus* are dominant species on farmlands in this area (Chen *et al.* 1998; Wang *et al.* 2003; Li *et al.* 2005). The current study demonstrates that water regulation by the TGR increased the habitability of the beaches of Dongting Lake for these 2 species. These 2 species might use the lake beaches because of their preference for damp habitats and their ability to swim. In general, *R. norvegicus* and *A. agrarius* are regarded as wetland or riparian specialists. Although *R. norvegicus* is mostly known as a communal animal that has an almost worldwide distribution in human settlements, it is also found in areas absent of human presence (Traweger *et al.* 2006). Even though rats also inhabit dry areas, they preferentially inhabit areas close to water, such as ponds, rivers and sewers (Traweger *et al.* 2006). Furthermore, rats are the only mammal to have successfully colonized the sewers and drainage systems of many urban environments (Heiberg *et al.* 2012). Harper *et al.* (2005) also confirm that *R. norvegicus* is associated with damp sites. Some studies suggest that *A. agrarius* is a wetland-loving species (Scott *et al.* 2008; Horváth *et al.* 2012). Furthermore, significantly higher numbers of *A. agrarius* were recorded in spring-flooded meadows during years of high flooding in the Nemunas River Delta, Lithuania (Balčiauskas *et al.* 2012). *S. murinus* and *M. minutus* are also associated with damp sites, whereas the other species recorded in the current study (*N. fulvescens*, *R. nitidus* and *E. europaeus*) were only occasionally caught in these areas. All of these species were recorded in habitats surrounding the lake beaches before the commencement of dam operations (Zhang *et al.* 2012b). The immigration of these species to the beach habitat during the dry season would result in a community structure that more closely resembles the rodent communities of the farmlands in this area.

A number of factors potentially influence the succession process of small mammal communities, including hydrological and meteorological parameters, vegetation succession, habitat suitability and interspecies relationships. Although some studies have found that riparian sites serve as source habitats for most small mammal species, the species richness of small mammals in riparian habitats is subject to variation (Andersen 1994; Ellison & van Riper 1998; Hanley & Barnard 1999). Extended periods of heavy flooding have more detrimental consequences on small mammals, although this factor might be buffered by the presence of refuges and the mobility of organisms. The disruptive consequences of floods depend on the water level, the duration of flooding and the speed of water level rise (McCarley 1959; Andersen *et al.* 2000). Anderson and Cooper (2000) found that the regulation of the Green River in the USA caused a reduction in the peak flood volume, which promoted the expansion of vole populations. Hence, the main reason for low species abundance on the Dongting Lake beaches before TGP might have been the extended periods of heavy flooding, which covered all lake beaches, and had a devastating effect on the small mammal community during summer. After the commencement of TGP operation, the water level of Dongting Lake might have been low during some rainy seasons, but might also have been high during some dry seasons, because of water regulation of the TGR (Ding & Li 2011). It has been stated that the greatest downstream consequence of river regulation on mammals is the disruption of the seasonal flood regime along rivers (Nilsson & Dynesius 1994; McCartney 2009). In our study, the hydrological and meteorological changes implemented through TGR operation might favor the small mammal community, resulting in higher species immigration to the beaches of Dongting Lake during the dry season. The possible underlying mechanism for such a shift in species distributions is the longer period of beach habitat exposure, which increases the opportunity for other species to establish home ranges and reproduce.

Vegetation succession might also contribute to changes in the small mammal community on the beaches. Anderson and Cooper (2000) found that river regulation might result in changes to riparian plant–herbivore relationships, because of shifts in river hydrology, which might promote a favorable herbaceous understory for voles. Furthermore, with an increase in altitude and decrease in flood time on the beaches of Dongting Lake, a greater extent of beach area became forested by *Populus* spp. (Xie & Chen 2008; Hou *et al.* 2011). In parallel, the species richness of the herbaceous layer increased, which would be expected to decrease the superiority rate of the superior species (Wu *et al.* 2005). Although we did not investigate plant–animal interactions on the beaches of Dongting after water regulation, we speculate that the continuous extension of forestland would favor small mammal communities. At least, these forests might serve as refuges for small mammals to escape death as a result of normal summer floods, or as an intermediary unflooded site to escape beach submergence. If rodents are able to find alternative nearby sites to take refuge, more rodents are likely to survive (Zhang *et al.* 2007b). This phenomenon has been reported at other wetlands (Stickel 1948; Wetzel 1958; McCarley 1959; Ellis *et al.* 1997; Williams *et al.* 2001). *R. norvegicus*, which is commonly assumed to avoid climbing, is actually adept at climbing. Foster *et al.* (2011) concluded that *R. norvegicus* seldom forages above ground, not because it cannot climb, but because arboreal foraging is more risky and less rewarding for this species. Furthermore, the project implemented to transform farmland back into lake habitats at the study site would also contribute to the reforestation of *Populus* in the Dongting Lake Region (Xie & Chen 2008; Hou *et al.* 2011); however, data from this project were not included in the current study.

Although we do not provide detailed analysis of the factors that affect the distribution and relative abundance of small mammals within the wetland landscapes, it might be concluded that Dongting Lake beach habitats have become suitable for harboring a broad variety of small mammal species, because of changes in habitat structure and composition (e.g. vegetation structure, habitat type, landscape composition, connectivity, substrate, moisture and size), in parallel to changes in flood regimes. Water regulation might potentially affect small mammal communities by altering habitat, in addition to changing species movement and survival patterns (Andersen 1994; Andersen *et al.* 2000; Falck *et al.* 2003). This study presents just an overview of the changes that have occurred in the small mammal community on the beaches of Dongting Lake after the commencement of TGR operation. We have yet to determine the exact factors that have led to the observed change in the small mammal community. Therefore, future research should focus on determining to what extent and in what way the TGP has contributed toward changing the structure of the small mammal community inhabiting the beaches of Dongting Lake. Further research on succession mechanisms, and the factors that influence succession, is required, through long-term surveys of the small mammal communities inhabiting the various habitats in the vicinity of the lake beaches.

Information about how the small mammal community repopulates after lake water levels decline in autumn is another very interesting issue. For example, the trap success for *A. agrarius* in the autumn of 2011 and 2012 was 3.5% and 0.3%, respectively. This difference in capture density might be linked to the extent of summer flooding. Flooding was a natural feature of the beaches at Dongting Lake prior to dam construction. However, the regulation of water by the TGP has modified the timing and quantity of water flow, which has caused the incidence of flooding to decline. Variation in the duration of beach submergence by flood water and different water levels in summer might, therefore, contribute to different baseline densities in the mammal community on the beaches after flood waters recede. The assimilation of long-term surveys, in parallel to more detailed analyses, is required to evaluate these issues.

In seasons when flooding would normally occur, small mammals occupying beach habitats would be forced to aggregate on the dikes, and migrate to farmland areas (Guo *et al.* 1997), with high population numbers potentially causing severe damage/losses to crops, as well as presenting a health hazard to humans. *A. agrarius* and *R. norvegicus* rarely inhabited the beaches before the commencement of the TGP operation, yet were found on all beaches after the commencement of TGR water impoundment, with steadily increasing population sizes. Therefore, it is important to monitor fluctuations in the populations of *A. agrarius* and *R. norvegicus*, in addition to *M. fortis*, to identify possible population outbreaks. In addition, shifts in the succession of the small mammal community structure on the beaches of Dongting Lake should be monitored, which may indicate potential trends leading to the outbreak of particular species.

Based on the index of diversity, the small mammal community on the beaches of Dongting Lake has already undergone major changes since 2003, with a tendency toward diversification. TGR water regulation has created a transitional small mammal community, characterized by the encroachment of species from areas surrounding the lake into *M. fortis*-dominated beach habitat. However, it remains unclear as to whether the observed changes will facilitate the control of rodent damage or whether the introduction of more species will generate greater damage to agricultural crops and human communities. Therefore, it is important to conduct studies on interspecies interactions.

The introduction of hydraulic structures to tributaries upstream of the dam has been suggested and trialed (Qiu 2012). Hence, it might be important to evaluate the additive impacts on the environment of placing successive dams along a single river (Berkun 2010; Zhai *et al.* 2010). The structure of the small mammal community at Dongting Lake might exhibit further changes in response to the superimposed effect of successive dams.

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