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Genetic variation of the striped hamster (*Cricetulus barabensis*) and the impact of population density and environmental factors

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Abstract

Background: The striped hamster (*Cricetulus barabensis*) is a dominant rodent species in the North China Plain and has suffered a continuous decline of population size in the last 17 years. However, little is known about the population genetic structure of this species and how it is influenced by geographical and environmental factors. In the present study, we investigated the genetic diversity and genetic differentiation of the striped hamsters in four geographical populations of different environmental features. The genetic variability for a sample of 158 animals from the four populations was estimated using data from 10 microsatellite loci.

Results: Genetic diversity exists in the striped hamster. The number of alleles and the proportion of heterozygosity indicate moderate variability. A total of 46 alleles were detected, with a moderate mean number of alleles. Significant genetic differentiation ($p < 0.01$) exists among all four examined geographical populations. Population-specific alleles and variable allelic richness were detected in all populations regardless of the geographical distances. The genetic diversity positively correlates with the population density, while the genetic distance is partially affected by the geographical distances. Moreover, the habitat environment is also an important factor influencing the genetic differentiation of the species.

Conclusions: The genetic diversity of the striped hamster is mainly impacted by population density, while partially influenced by geographical distances. The results of our study and other studies collectively suggest that a minimum geographical distance is required to prevent gene flow between different populations and for genetic differentiation to be pronounced.

Keywords: Population genetic structure; Genetic diversity; Genetic differentiation; The striped hamster; Population density; Microsatellite

Background

Population dynamics is a central issue in population ecology and varies greatly as a result of the interplay of genetic factors and environmental factors. Anthropogenic activities have imposed increasing impact on habitats and ecosystems of wildlife, and consequently, many species are suffering from decreasing population sizes (Liu et al. 2013). Genetic diversity is a key evolutionary variable that correlates with population size and is believed to be critical for population viability and the persistence of species. It is affected by a number of evolutionary processes such as selection, gene flow, genetic drift, and dispersal patterns. Loss of genetic diversity of a population may result in declined fitness and the ability to persist and adapt in ever-changing environments (Garant et al. 2007; Lenormand 2002). Therefore, maintenance of genetic diversity is fundamental for wildlife conservation and management, and analysis of population genetic structure and the influencing factors in wild populations is the first step.

The striped hamster (*Cricetulus barabensis*), also known as the *striped dwarf hamster*, is one of the dominant rodent species in the North China Plain. It is also distributed in Russia, Mongolia, and Korea. The hamsters feed on stems and leaves of plant during summer and on foraging crop seeds in winter (Zhao et al. 2013). They are solitary and very aggressive and have been widely used as

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laboratory animals. Though considered a pest, the species has experienced a continued decline of the population density in the last 17 years, which is attributed mainly to agricultural activities (Yan et al. 2013). Various approaches have been used to forecast the population dynamics of the striped hamster (Wu et al. 2007a, b). Most research, however, have focused on the environmental and anthropogenetic factors (Hou et al. 1993; Song and Wang 2003; Yan et al. 2013), while the population genetic structure of the striped hamster is poorly understood. The application of mixed methods of evaluating patterns of individual genotypes, allele frequencies, and genetic structure is becoming a powerful means for descriptive genetic analysis. Such methods are being increasingly used for inference of population structure at the landscape scale, as is needed to forecast population dynamics. Effective strategies to forecast and control the abundance of the striped hamster incorporate an understanding of their present genetic structure and the distribution of genetic diversity throughout the geographical range. To date, however, there have been few such efforts to forecast population dynamics from patterns of genetic variation in the striped hamster (Xu et al. 2008). Large-scale studies of the population genetics of the striped hamster have not been carried out.

Polymorphic microsatellite loci are the most frequently used and the most informative molecular markers for analysis of genetic diversity and genetic differentiation (Kim and Sappington 2013). In the striped hamster, 14 microsatellite markers have been isolated and characterized (Xu et al. 2008). In the study, the authors analyzed the genetic diversity of the striped hamsters and detected no significant allelic variations among different populations of the striped hamster. The lack of genetic diversity may be explained by the short distance among the sampling locations (60 km) where no geographical barrier exists to prevent gene flow. Until now, no factors influencing genetic variation have been analyzed.

In the present study, by examining ten microsatellite loci, we investigated the population genetic structure of the striped hamsters from four geographical locations that are 167 to 945 km apart and of different environmental features. The four populations were from Wucun (W), Pingyi (P), Xilinhaote (X), and Zhenglanqi (Zh) Counties of the North China Plain. We aimed (1) to reveal the genetic diversity of the striped hamsters in different geographical locations, (2) to examine the genetic differentiation among the geographical populations, (3) to analyze the relationship between the geographical and genetic distance, and (4) to compare the correlation between the genetic diversity and population density of the striped hamster to provide a basis for the conservation and management of population dynamics.

Methods

Ethics statement

All hamster procedures were reviewed and approved by the Institutional Animal Care and Use Committee of the Institute of Zoology, Chinese Academy of Sciences (Permit Number: IOZ11012) and by the Ethics Committee of Qufu Normal University. All researchers and students had received appropriate training and certification before performing animal studies.

Sample collection and DNA extraction

We captured striped hamsters using live traps made of wire mesh in the grassland areas of W, P, and X Counties and in the sandy area of Zh County of the North China Plain at the autumn of 2007. Previous studies suggest the need for sample sizes of at least 20 individuals to obtain accurate estimates of genetic distance (Kalinowski 2004). The sample size of each population in this study meets its requirements. One hundred and fifty-eight individuals were analyzed in this study, comprising 42 from W, 44 from P, 38 from X, and 34 from Zh. The rates of live traps, which represent population density (Yan et al. 2013), were 4.8%, 5.2%, 7.1%, and 1.2% in W, P, X, and Zh populations, respectively. The sampling locations in the present study are shown in Figure 1.

An approximate volume of 0.1 mL blood was taken from the lateral tail vein of each individual and preserved in 95% ethanol. Whole genomic DNA was extracted using standard phenol-chloroform protocols and preserved in 95% ethanol (Sambrook and Russell 2006). In order to prevent contamination during DNA extraction, benches and plasticware were cleaned with 10% bleach and sterile water and then exposed to ultraviolet (UV) light for 30 min. The surface of muscle samples was also exposed to UV light for 30 min. DNA samples were stored at −20°C for further microsatellite genotyping. We used ten extraction controls, and none produced positive amplification during subsequent polymerase chain reaction (PCR).

Microsatellite genotyping

Ten microsatellite loci for *C. barabensis* (Song et al. 2011; Xu et al. 2008) were used for this study on the basis of their efficiency. Variation at each locus was assessed by PCR. Amplification reactions were carried out in a total volume of 25 μL containing 2.5 μL of 10× PCR buffer, 2.5 mM $MgCl_2$, 0.2 nM dNTP, 1 U *Taq* DNA polymerase (Promega Corporation, Fitchburg, WI, USA), 10 pM of forward and reverse primers, and approximately 2 ng of template DNA using the following temperature profile: 5 min at 94°C; followed by 30 cycles of 45 s at 94°C, 45 s at 46°C to 58°C, and 30 s at 72°C; followed by a final extension of 10 min at 72°C; and storage at 4°C. After amplification, PCR products were diluted and genotyped on a

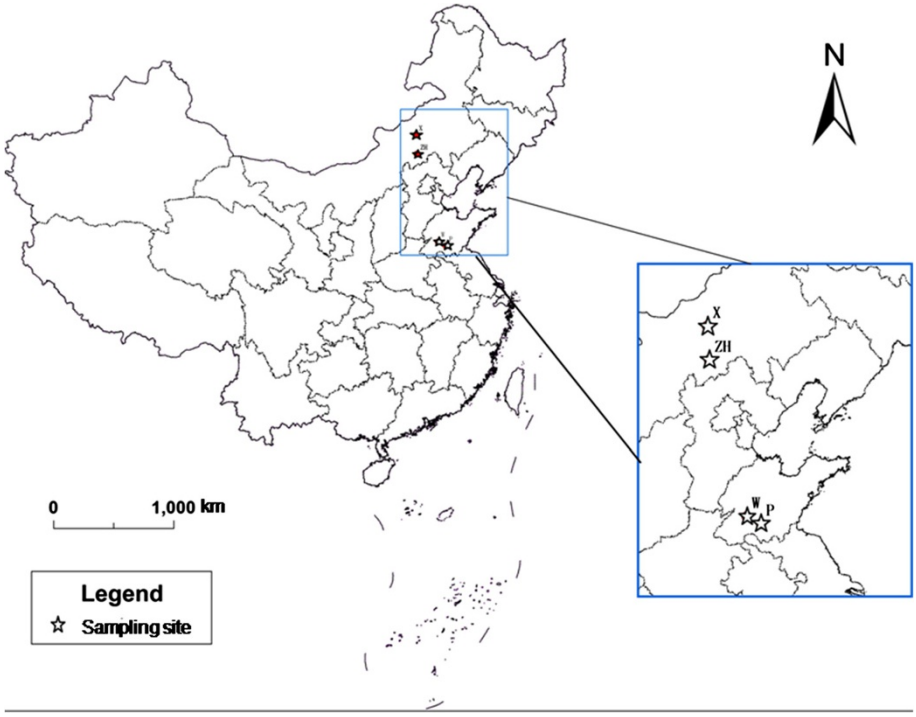

Figure 1 Map of sampling locations of the present study. The four sampling sites are Wucun (W), Pingyi (P), Xilinhaote (X), and Zhenglanqi (Zh) Counties of the North China Plain. W and P are in Shandong province, while X and Zh are in Inner Mongolia.

Beckman CEQ8000 (Beckman Coulter, Inc., Brea, CA, USA) according to the manufacturer's instructions using CEQ8000 software and GeneMarker version 1.5 (SoftGenetics, State College, PA, USA).

Data analysis

Analysis of molecular variance (AMOVA) was used to examine the diversity of the striped hamster within and among the populations using a microsatellite marker. AMOVA tests were hierarchical and used 1,000 permutations as implemented in Arlequin to test whether each of the two levels of organization (within and among populations) explained a significant portion of the overall microsatellite diversity.

Diversity was analyzed per locus and per population on the basis of allelic richness (R_S, number of alleles independent of sample size), observed (H_O) and expected (H_E) heterozygosity, and linkage disequilibrium. All calculations were performed in FSTAT (Goudet 1995) with significance based on Bonferroni-corrected P values after 10,000 random permutations. Deviations from Hardy-Weinberg equilibrium (HWE) for each population were assessed using an exact test implemented in GENEPOP (Raymond and Rousset 1995).

To compare population-level relationships identified by microsatellite markers, we constructed neighbor-joining (NJ) dendrograms based on pairwise genetic distances. NJ dendrograms for microsatellites were constructed in NEIGHBOR and PHYLIP version 3.5 (Felsenstein 1993). Support for microsatellite Nei's distance dendrogram was based on 1,000 replicate distance measures constructed in MSA by permuting genotypes among populations (Dieringer and Schlotterer 2003).

Genetic differentiation between geographical populations was assessed by comparing the average number of pairwise differences between different populations (PiXY), the average number of pairwise differences within populations (PiX and PiY), and the corrected average pairwise difference (PiXY – (PiX + PiY)/2) using Arlequin 2.000.

Results

Microsatellite polymorphisms

A total of 46 alleles were detected using the 10 microsatellite loci from 158 individuals (W 42, P 44, X 38, Zh 4), with a mean allele number per locus of 4.6 (range 1.70 in Zh to 2.30 in X). While some alleles were more restricted, the others showed a wide geographical distribution (shown in Additional file 1: Table S1). Twenty-one of 46 alleles were found in only a single population. Among the ten loci, the number of alleles observed per locus varied from two (EF543185) to six (DQ459487, DQ459492, DQ459494, EF543179, EF543177, and EF543186), as shown in Additional file 1: Table S2.

Table 1 Average gene diversity over loci based on the number of different alleles

	Populations			
	W	P	X	Zh
Gene diversity	0.40 ± 0.23	0.43 ± 0.24	0.52 ± 0.28	0.29 ± 0.17
Trap success, %	4.8	5.2	7.1	1.2

Estimates of allelic richness (R_S), observed (H_O) heterozygosity, and expected (H_E) heterozygosity for the microsatellites in each population are shown in Additional file 1: Table S3. Allelic richness in the X population was higher and ranged from 3.8 to 4.9 alleles per locus (average = 4.1). Polymorphism was moderate in W and P populations with allelic richness ranging from 1.0 to 3.7 alleles per locus (average = 2.7) and from 1.0 to 4.0 alleles per locus (average = 2.7), respectively. In the Zh population, average allelic richness (average = 1.6) per sample over all loci was lower compared to that in the other examined populations.

Observed heterozygosity ranged from 0 to 0.81 (average = 0.35), with the lowest average value (average = 0.25) for the Zh population and the highest average value (average = 0.44) for the X population. Expected heterozygosity ranged from 0 to 0.67, with the lowest average value (average = 0.29) for the Zh population and the highest average value (average = 0.52) for the X population.

After Bonferroni correction, all ten loci significantly deviated from HWE in the X population, EF543178 loci in the W population, and EF48900 loci in the P population. All ten loci were within HWE in the Zh population.

Diversity indices, average gene diversity over loci, are summarized in Table 1. Higher genetic diversity (0.52) was found in the X population while moderate in W (0.40) and P (0.43) populations and lower in Zh (0.29) population. The genetic diversity was positively related to the rate of live traps (Figure 2), which represent the population densities.

Genetic differentiation

Allele distribution displays certain geographical specificity (Additional file 1: Table S2). Allele 330 at DQ459487 loci, allele 309 at DQ459492 loci, allele 391 at EF543179 loci, allele 380 at EF543177 loci, allele 182 at EF543178 loci, and allele 348 at EF530613 loci were detected only in the W population. Population P also possesses the following specific alleles: 315 at DQ459492 loci, 404 and 484 at EF543179 loci, 392 and 450 at EF543177 loci, and 400 at EF543186 loci. The specific alleles that only exist in the X population were 335 at DQ459487 loci, 390 and 406 at DQ459494 loci, and 280 and 330 at EF543177 loci. Allele 345 at DQ459487, allele 330 at DQ459492, allele 406 at EF543179, and allele 200 at EF543186 were specific alleles in the Zh population. Meanwhile, the tested populations possess some common alleles shown in Additional file 1: Table S2.

The test of population differentiation showed that these four geographical populations are significantly differentiated from each other in pairwise comparisons ($p < 0.001$) (Table 2).

Analyses of population genetic structure

Genetic and geographical distances among the examined populations are summarized in Table 3. A higher genetic distance was found between Zh and W (2.35) and Zh and P (1.68) populations. The genetic distance between X and Zh populations was moderate (0.74). The genetic distances among W, P, and X populations were lower (0.62 to 0.63). The geographical distances, based on the electronic map, are also listed in Table 3. The correlation

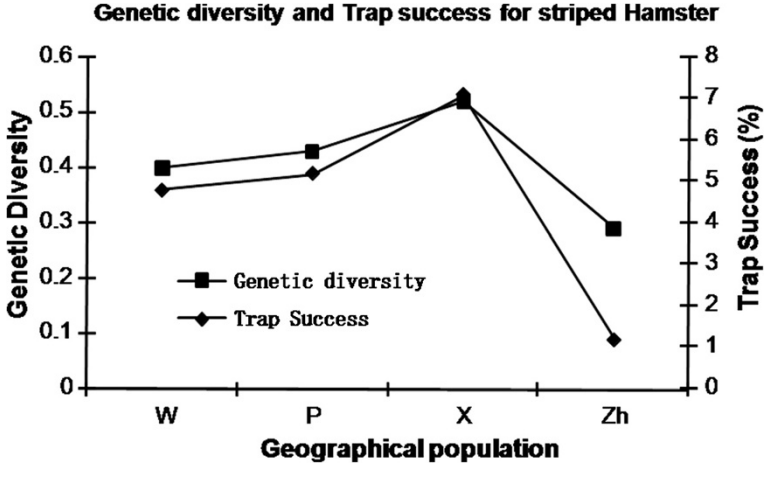

Figure 2 Correlations between genetic diversity and the rate of live traps. Live trap success is expressed as the percentage of live traps. Genetic diversity represents the frequency of alleles corresponding to Table 1.

Table 2 Pairwise genetic differentiation for microsatellite data of the striped hamster based on Nei's distance method

Populations	W	P	X	Zh
W	4.04	6.84 ($p = 0.000$)	7.04 ($p = 0.000$)	9.48 ($p = 0.000$)
P	2.68 ($p = 0.001$)	4.28	7.27 ($p = 0.000$)	8.81 ($p = 0.000$)
X	2.40 ($p = 0.001$)	2.51 ($p = 0.001$)	5.23	7.10 ($p = 0.000$)
Zh	6.01 ($p = 0.000$)	5.22 ($p = 0.000$)	3.03 ($p = 0.001$)	2.89

Above diagonal: average number of pairwise differences between populations (PiXY). Diagonal elements: average number of pairwise differences within populations (PiX). Below diagonal: corrected average pairwise difference [PiXY – (PiX + PiY)/2]. Corrected average pairwise differences, which are statistically different, are indicated.

between the genetic and geographical distances is shown in Figure 3.

NJ analysis of populations based on standard genetic distance, firstly, produced two groups: A (W, P, and X populations) and B (Zh population). Secondly, A group could be subdivided into two subgroups: 1 (X) and 2 (W and P) as shown in Figure 4.

relationship between genetic diversity and the influencing factors, including population density, geographical distance, and environmental factors, is discussed below.

Discussion

Genetic diversity and genetic differentiation

Geographical variation in population genetic structure across species' ranges is critical for the environmental adaptation and evolution of the species. The importance of genetic diversity for the viability of populations is widely accepted (Frankham et al. 2010; Hansson and Westerberg 2002; Reed and Frankham 2003; Schmitt and Hewitt 2004). Genetic diversity and differentiation of populations are dictated by the interplay of genetic drift, gene flow, and natural selection. Variation in population turnover and population size may have a major impact on these processes. Gene flow, determined by the mobility of the species and geographical distance, promotes genetic diversity and precludes differentiation, while selection and drift enhance genetic differentiation if populations are sufficiently isolated. As the isolation of population increases and the population size reduces, genetic drift and inbreeding depression become more influential than gene flow, and the differentiation among populations is expected to become greater and more variable. Greater genetic diversity, represented by allele richness and degree of heterozygosity, correlates significantly with fitness.

Table 3 Geographical and genetic distances among different populations

Populations	W	P	X	Zh
W		0.63	0.63	2.35
P	167		0.62	1.68
X	931	945		0.74
Zh	748	766	185	

Above diagonal: genetic distance. Below diagonal: geographical distance (km).

Among the examined geographical populations in our study, there exist significant genetic differences. Population-specific alleles and variable allelic richness were detected in all populations regardless of the geographical distances. This may be attributed to the species' relatively restricted mobility and habitat availability in the local area, whereby selection and genetic drift may be important factors influencing population genetic characters. In another report (Xu et al. 2008), no significant differences in genetic variation were detected among the three striped hamster populations that were only 60 km apart. In our study, the shortest distance between two populations is 185 km, which is much greater than that in the study by Xu et al. Thus, it appears that a minimum distance (between 60 and 185 km) between two populations is a prerequisite for genetic differentiation to be pronounced.

Two commonly used indices of genetic diversity, allelic richness, and heterozygosity (observed and expected heterozygosity, H_O and H_E, respectively) for the microsatellites in the examined populations are in the same order of X > P > W > Zh populations. Correspondingly, the density of the populations was in the similar sequence of X > P > W > Zh populations. As shown in Figure 2, an obvious correlation can be inferred between the levels of genetic diversity and the population density. Our results are in accordance with studies in other species in which a similar correlation was found (Aspi et al. 2006; Berthier et al. 2006; Eckert et al. 2008; Frankham 1996; Furlan et al. 2012; Montgomery et al. 2000; Wang et al. 2013), including other rodents (Krebs 2013) and hamster species (Romanenko et al. 2007), like the greater long-tailed hamster (Dong et al. 2010; Xie and Zhang 2006; Xu et al. 2013a; Xue et al. 2014), the golden hamster (Karsten et al. 2005), and the common hamster (Banaszek et al. 2012; Neumann et al. 2005). Similarly, the genetic diversity of the striped hamster has experienced a trend of continuous decline in recent years. However, the genetic distance of the striped hamster correlates partially with geographical distance, while it is more greatly influenced by environmental factors. Strong fluctuations in population density can lead to loss of genetic diversity, and

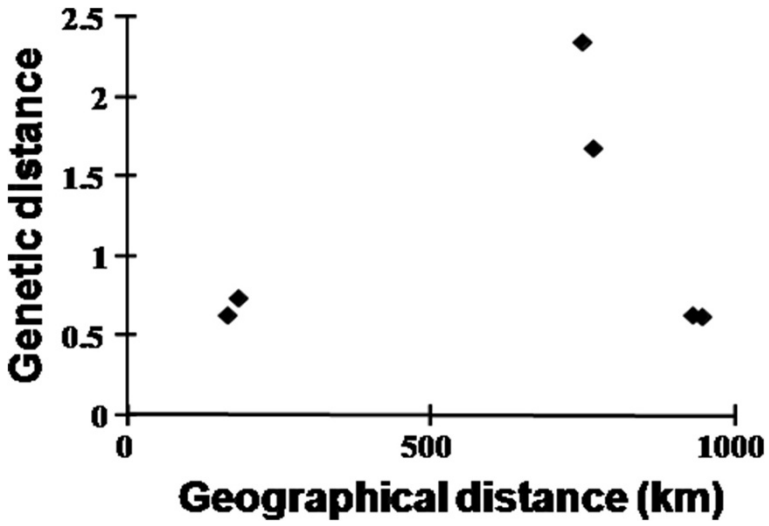

Figure 3 Correlations between genetic distance (measured as Nei's (1978) genetic distance) and geographical distance. Genetic distance values are corresponding to those in Table 3.

in return, reduction in genetic diversity and inbreeding depression can significantly lower the ability of populations to adapt to changing environments, eventually leading to extinction (Frankham 1996). Therefore, maintenance of genetic diversity is an essential issue of conservation.

Population structure

Microsatellite DNA data for the striped hamster revealed significant genetic polarization among populations, with deep genetic divergence between the two lineages (A and B), as shown in Figure 4. The examined populations based on geographical distance could be divided into clusters I (W and P) and II (X and Zh), which was in discrepancy with the genetic analysis and implying that genetic distance was not positively correlated with geographical distance (Figure 3). The common character of the populations in lineage A is that their habitat environments were all grassland areas, while the habitat environment of the Zh population in lineage A was a sandy area. The populations based on its habitat environments could be partitioned into two lineages: a (X, W, and P) and b (Zh), which was in accordance with the results of genetic analysis and implying that habitat environment is an important factor influencing its genetic differentiation. A previous study showed that different living condition is a reason leading to genetic differentiation among populations (Wang et al. 2008), which was in accordance with the results of this study.

The lineage A based on genetic distance could be subdivided into two subgroups: 1 (X) and 2 (W and P populations), which was in accordance with the result analyzed by the geographical distance. Therefore, isolation by distance (IBD) may partly account for the genetic differentiation among W, P, and X populations, which was in accordance with the results of former scientists (Jiang et al. 2007; Xu et al. 2013b; Zi-Yan 2008).

That lineage B (population Zh) is greatly differentiated from the other populations raises the possibility to classify the Zh population as a subspecies. Currently, subspecies

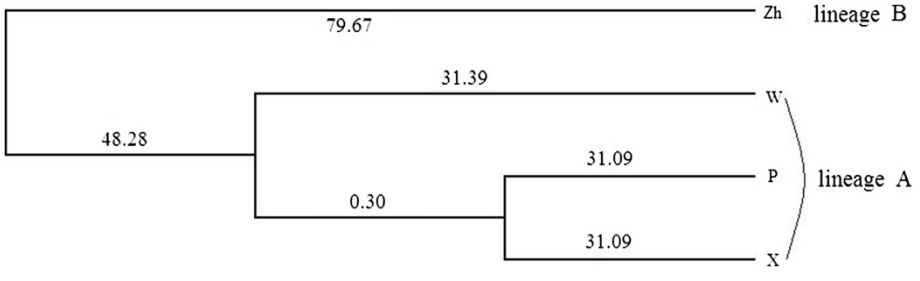

Figure 4 NJ tree based on Nei's (1978) genetic distance by the method. Modified from the NEIGHBOR procedure of PHYLIP version 3.5. All populations are marked. Bootstrap values are shown.

are defined by a combination of morphological, behavioral, and genetic characters, among which phylogenetic distinction is considered to be essential (Haig et al. 2006). However, these criteria have not been applied to hamsters, and a standard of how large the genetic distance to define a hamster subspecies is lacking. We have not observed any morphological or behavioral differences between the Zh population and other populations. In light of the phylogenetics to define subspecies in other species, such as birds (Phillimore and Owens 2006), the genetic distance of lineage B is large enough to define the Zh population as a subspecies. Intriguingly, the geographical distance between Zh and X populations appears to be close enough for genetic interactions and no barrier exists to prevent gene flow, yet they show distinct phylogenetic patterns. The highest differentiation and lowest genetic diversity that correlate with the lowest population density are implicative of inbreeding depression within the Zh population. We believe that a more extensive sampling, including regions of Mongolia and Korea, should provide a more complete picture of the morphological, behavioral, and phylogenetic patterns of the striped hamster and to precisely define subspecies.

The genetic differentiation within the breed resulted from the interactions of genetic and environmental factors. Gene flow belongs to genetic factors, which is variably affected by geographical distance, habitat fragmentation, and so on. Habitat environment belongs to environmental factors such as grassland and sandy areas, which plays an important role in selection. Genetic diversity and ecological factors can have reciprocal influences (Hughes et al. 2008). Genetic diversity impacts significantly on ecological processes such as primary productivity, population recovery from disturbance, interspecific competition, community structure, and fluxes of energy and nutrients. In return, ecological and environmental factors can also play a role in shaping genetic diversity patterns (Gaggiotti et al. 2009). Based on the above analysis, genetic differentiation within the striped hamster was caused by the interaction of genetic and environmental factors, in which environmental factors play a more important role.

Conclusions

We have, for the first time, systematically analyzed the population genetic structure of the striped hamsters and the influencing factors. Our data revealed that there is a moderate level of overall genetic diversity (allele richness and heterozygosity) and significantly different genetic variation among the studied populations. The genetic diversity is positively correlated to the population density and is greatly affected by the environmental factors, while geographical isolation by distance contributes partially to the genetic differentiation among the different populations. In addition, the results of our study and other studies collectively suggest that a minimum geographical distance (between 60 and 185 km) is required for genetic differentiation to be pronounced. Our data provide the first empirical evidence for the existence of genetic differentiation and the influencing factors in the striped hamster.

Additional file

Additional file 1: Table S1. Genotypes of ten microsatellite loci for the four examined geographical populations of striped hamster. **Table S2.** Alleles examined in the striped hamster at ten microsatellite markers for different geographical populations. **Table S3.** Allelic richness, observed heterozygosity, and expected heterozygosity at ten microsatellite markers for different striped hamster populations.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

HLX and LXX conceived the study. HLX designed the study. JHX performed the experiments and acquired the data. LC analyzed the data. LC and HLX performed the statistical analysis. HLX and JHX prepared the manuscript. LXX and LC edited the manuscript. LXX reviewed the manuscript and guaranteed the integrity of the entire study. All authors read and approved the final manuscript.

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