



Article Genetic Diversity and Relatedness of Group-Living Small Mammals on the Mongolian Plateau

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Abstract: Genetic diversity plays an important role in the evolution and adaptation of organisms. Losses of genetic diversity make organisms more vulnerable to climate changes and diseases, reducing the viability of small populations. In addition to natural selection, genetic drift, dispersal, inbreeding, and population bottleneck, the social systems of animals may also affect the genetic diversity of populations. We aimed to test the hypothesis that the delayed dispersal of group-living small mammals would reduce genetic diversity through attenuated gene flow but enhance genetic relatedness. We used microsatellite analysis to estimate genetic diversity and the Queller and Goodnight relatedness coefficients of Daurian pikas (Ochotona dauurica) and Mongolian gerbils (Meriones unguiculatus), two socially monogamous small mammals living in social groups in Inner Mongolia, China. The average genetic relatedness of social groups was inversely related to the average genetic diversity of social groups in Daurian pikas but not in Mongolian gerbils, partially supporting our hypothesis. Dispersal following frequent local extinctions resulted in the recolonization of burrow systems by individuals with different genetic makeups, increasing genetic diversity and reducing the genetic relatedness of the social groups of Daurian pikas. On the other hand, delayed short-distance dispersal was sufficient to maintain the high genetic diversity and high genetic relatedness of gerbil social groups independently.

Keywords: dispersal; *Meriones unguiculatus*; microsatellite analysis; *Ochotona dauurica*; social group; social monogamy

1. Introduction

Genetic diversity is the raw material of natural selection and determines the adaptation of species to environmental changes [1,2]. High genetic diversity improves the resistance of species to diseases and the viability of small populations [2–4]. Therefore, genetic diversity is an integral component of biodiversity. Genetic diversity is primarily affected by natural selection, genetic drift, gene flow via dispersal (or migration), population bottleneck, and reproduction mode [2,5]. Life history traits may also affect genetic diversity by influencing effective population sizes [5].

Social systems of animals such as mating systems and social organization may influence the effective population size (e.g., through the deviation from equal reproductive contributions and changes in sex ratio) and dispersal [5]. Social organization can exert significant effects on the genetic diversity of social organisms. For instance, the delayed dispersal of juveniles forms social groups, increasing genetic relatedness within social groups [6]. Kinship, or genetic relatedness, is a key factor influencing the evolution of social groups [7]. Inclusive fitness through kinship or genetic relatedness promotes the formation and maintenance of group living when the indirect benefits of delayed natal dispersal or



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). living in groups outweigh the costs of group living [7]. It is plausible to predict an inverse relationship between genetic relatedness and genetic diversity unless gene flow between social groups enhances genetic diversity. On the other hand, group-living rodents like Mongolian gerbils (*Meriones unguiculatus*) may exhibit group territoriality to defend against immigration or even those merely passing through their territories [8,9]. Such territoriality may become a social barrier to gene flow (i.e., isolation by social resistance) [10]. It is unknown whether kinship-based group living results in similar relationships between genetic diversity and the relatedness of social groups in different species.

The Daurian pika (*Ochotona dauurica*) and Mongolian gerbils are two group-living small mammals commonly found in the grassland on the Mongolian Plateau [11,12]. Daurian pikas are believed to be socially monogamous [13] and reproduce from April to August [14,15]. Unlike the pikas in North America [13], Daurian pikas live in social groups year-round [11]. A social group consists of 2–5 individuals in Inner Mongolia (G.M. Wang, personal observation). Populations of Daurian pikas undergo frequent local extinctions during winter [16], which makes it difficult to conduct long-term studies of the behavior and population of this species. It is possible that the dispersal and recolonization of burrow systems by different individuals with different genetic makeups result in an inverse relationship between the genetic relatedness and genetic diversity of Daurian pika social groups. To the best of our knowledge, little is known about the genetic relatedness and genetic diversity of the social groups of Daurian pikas.

Mongolian gerbils are social rodents distributed on the typical steppes, desert grasslands, and agricultural fields on the Mongolian Plateau [12]. Mongolian gerbils also live in groups, each consisting of 2–17 individuals possibly as an extended family group [17,18]. Mongolian gerbils are also believed to be socially monogamous [19]. Juvenile gerbils often delay their natal dispersal, remaining at their natal sites after weaning [17,20]. The average genetic relatedness of the social groups of Mongolian gerbils is 0.28 (95% CI: 0.23–0.34), and dispersal between social groups results in a significant spatial population genetic structure [6]. However, relationships between the genetic diversity and relatedness of Mongolian gerbil social groups remain unknown. Furthermore, it is unclear whether a similar group-living behavior results in similar genetic diversity–relatedness relationships between Daurian pikas and Mongolian gerbils.

In this work, we tested the hypothesis that the delayed dispersal of group-living small mammals reduces genetic diversity through the attenuation of gene flow but enhances genetic relatedness, resulting in an inverse relationship between genetic diversity and relatedness. Alternatively, we hypothesized that gene flow or dispersal between social groups is sufficient to maintain sufficiently high genetic diversity in the social groups of small mammals, with the genetic diversity of social groups being independent of genetic relatedness. We carried out a microsatellite analysis of the genetic diversity and relatedness of Daurian pikas. We also reanalyzed the microsatellite genetic data of Mongolian gerbils from Wang, Liu, Wang, Zhong, and Wan [6] to test the two hypotheses.

2. Methods

2.1. Study Areas

We carried out a capture–recapture study of Daurian pikas in Naren, Abaga Banner (county), in the grassland of northcentral Inner Mongolia, China (44°26′ N, 114°58′ E, 1130 m elevation). The climate is semi-arid, with mean annual total precipitation ranging from 135.0 to 267.2 mm. Monthly mean temperatures varied from –22.9 to 23.6 °C. Snow cover lasted from mid-to-late October to early May. Vegetation on the study site mainly consisted of *Leymus chinense, Artemisia frigid, Allium polyrhizum, Salsola collina,* and *Chenopodium glaucum* [21].

We reanalyzed the microsatellite genetic data of Mongolian gerbils from Wang, Liu, Wang, Zhong, and Wan [6] to test the two alternative hypotheses. We live-trapped Mongolian gerbils at Xima Gou (115°22′ E, 42°07′ N, 1450 m elevation), located in a typical steppe intermixed with the semi-arid climate cropland in Taipusi Qi (county), Inner Mongolia, China. Average monthly temperature ranged from -19.1 to 21.1 °C. Average annual total precipitation ranged from 258 to 550 mm [22]. Daurian pikas and Mongolian gerbils coexist in our study areas [12].

2.2. Live-Trapping of Daurian Pikas and Mongolian Gerbils

We live-trapped Daurian pikas biweekly on a 1.5 ha plot (140 m \times 110 m) from 12 May 2010 to 28 October 2010; from 10 July 2011 to 11 October 2011; and from 20 May 2012 to 5 October 2012. We did not trap Daurian pikas during winter to avoid trap mortality resulting from low temperatures [21]. Our trapping plot had 30 Daurian pika burrow systems. We placed a wire-mesh live trap (28 cm \times 13 cm \times 10 cm) at each active burrow entrance in each of the 30 burrow systems, with 8–12 traps per burrow system and a total of 350–400 traps each trapping week. We live-trapped Daurian pikas from 0500 h to 1900 h, with traps being closed from 1100 h to 1500 h to avoid trap mortality resulting from heat stress from June to August. Traps were checked every one or two hours. In May, September, and October, the months of lower temperatures, living-trapping was carried out from 0630 h to 1730 h to avoid trap mortalities due to extremely low temperatures in the early morning and late afternoon during those months [21].

Each captured pika was marked with an ear tag with a unique identification (ID) number (S. Roestenburg Inc., Herriman, UT, USA) upon its initial capture. We also sexed captured pikas and weighed them to the nearest 0.1 g with a portable electronic scale (Scout SE601F, Ohaus Corp., Parsippany, NJ, USA). The ID number, trap location (i.e., burrow system ID), sex, and body mass of each capture were recorded. We cut a small piece (2 mm \times 2 mm) of ear biopsy from each captured pika for DNA extraction. Captured pikas were released at the same trap stations of the captures immediately after handling.

Our trapping plot of Mongolian gerbils was situated on a 9 ha grassland (300 m × 300 m) surrounded by wheat (*Triticum* spp.) and cabbage (*Brassica* spp.) crop fields. The vegetation was dominated by the grass *Leymus chinense* and the herb *Corispermum mongolicum* and included a mixture of grasses such as *Cleistogenes squarrosa* and *Setaria viridis;* the herbs *Artemisia sieversiama, Artemisia scoparia,* and *Heteropappus altaicus;* and the small shrubs *Caragana microphylla* and *C. korshinskii.* We live-trapped Mongolian gerbils from 28 burrow systems using the same capture-recapture methods as those for trapping Daurian pikas from 28 April to 21 October in 2006 at 2-week intervals [22]. We clipped 1 toe per foot, removing half a toe at the joint with a pair of sharp, thin-bladed scissors from each captured gerbil for the microsatellite DNA analyses [6].

2.3. Microsatellite Analysis

We extracted genomic DNA from the ear tissue samples of captured pikas using phenol-chloroform extraction methods after Sambrook and Russell [23]. The quality and quantity of extracted DNA were visually examined on agarose gels stained with ethidium bromide. We used cross-species amplifications of 11 microsatellite markers to genotype captured pikas with polymerase chain reactions (PCR). Of the 11 markers, ocp1, ocp2, ocp3, and ocp5 were originally developed for O. princeps [24]; occ02 for O. collaris [25]; and p7F, p47F, p124R, p149F p156F, and p172F for O. curzoniae [26]. We used the same PCR reaction conditions and protocol for each marker as in Peacock, Kirchoff, and Merideth [24]; Li, Geng, Yang, Zhang, and Hu [26]; and Zgurski, Davis, and Hik [25]. Amplified fragments were electrophoresed on an ABI PRISM 377 automated sequencer (Applied Biosystems, Foster City, CA, USA), and were scored using Genescan[®] Version 3.7 (Applied Biosystems). We genotyped each pika sample twice independently to assess typing error rates. If differences occurred between two genotyping runs, we continued genotyping until a consensus was reached. We assessed null alleles, short allele dominance, and typing errors associated with stutter using the program MICRO-CHECKER [27]. We tested the Hardy–Weinberg equilibrium (HWE) at each locus and linkage disequilibrium (LD) between each pair of loci using the program GENEPOP 3.4 with the Markov chain option of 50 batches and

100,000 iterations per batch [28]. We used the Bonferroni correction for multiple comparisons with a nominal significance level of 0.05 in the LD assumption test.

We extracted DNA from the toe tissues of gerbils using the same phenol–chloroform extraction methods. We visually examined the quality and quantity of extracted DNA on agarose gels stained with ethidium bromide. We genotyped 327 gerbils from 28 social groups using nine microsatellite markers, *Mungµ1*, *Mungµ2*, *Mungµ3*, *Mungµ4*, *Mungµ5*, *Mungµ6*, *Mungµ7*, *Mungµ8*, and *Mungµ9* [29]. We assessed genotyping errors and tested the HWE and LD assumptions using the same methods as those for Daurian pikas (see [6] for details).

We defined a social group as the individual Daurian pikas or Mongolian gerbils that were live-captured in the same burrow system. We calculated the mean numbers of alleles per locus, average observed and expected heterozygosity at each locus, average Shannon diversity index, and mean pairwise Queller and Goodnight (QG) relatedness coefficients [30] with 999 iterations by social group using the program GENALEX 6.4 [31]. We used the Shannon diversity index as the genetic diversity index for the social groups of Daurian pikas and Mongolian gerbils.

2.4. Statistical Analysis

We used the linear regression of the average Shannon diversity index against mean the QG relatedness coefficient to test our hypothesis that the average genetic diversity of social groups decreases with increased genetic relatedness due to delayed dispersal. We used R v. 4.2.0 to carry out the linear regression [32].

3. Results

All 11 microsatellite loci were successfully cross-amplified in 194 Daurian pikas. The HWE at each locus and LD assumptions were met at a significance level of 0.05 with the Bonferroni correction in 30 social groups of Daurian pikas. The genetic diversity of the microsatellite loci was high with the expected heterozygosity (H_e) ranging from 0.55 to 0.93 (Table 1). The Shannon diversity index of microsatellite genetic diversity was inversely related to the average QG genetic relatedness coefficient of the Daurian social groups (slope = -1.09, p = 0.02, df = 24, $R^2 = 0.21$, Figure 1a). However, genetic diversity was not related to the average genetic relatedness of the Mongolian gerbil social groups (slope = 0.35, p = 0.78, df = 24, $R^2 = 0.003$, Figure 1b). Social groups of Mongolian gerbils consisted of more related individuals than did those of the Daurian pika social groups (t = -4.0412, df = 38, p = 0.0003, Figure 2a,b).



Figure 1. Relationships between the genetic relatedness (Queller and Goodnight coefficients) and genetic diversity (Shannon diversity index) of (a) Daurian pikas and (b) Mongolian gerbils in Inner Mongolia, China. The letter β is the estimate of regression slope.



Figure 2. Distributions of the Queller and Goodnight genetic relatedness coefficients for social groups of (**a**) Dauria pikas and (**b**) Mongolian gerbils in Inner Mongolia, China.

Table 1. Summaries of allelic diversity and heterozygosity for 11 microsatellite markers crossamplified in Daurian pika, Inner Mongolia, China.

	occ2	ocp1	ocp2	ocp3	ocp5	p7F	p47F	p124R	p149F	p156F	p172R
Number of alleles	10	6	7	19	17	26	14	19	31	8	25
Number of effective alleles	4.01	2.23	3.58	9.67	8.52	14.47	10.87	10.10	13.74	2.78	10.69
Shannon diversity index	1.66	1.00	1.50	2.49	2.35	2.86	2.49	2.48	2.91	1.43	2.68
Observed heterozygosity (Ho)	0.68	0.58	0.49	0.68	0.80	0.50	0.82	0.79	0.68	0.42	0.84
Expected heterozygosity (He)	0.75	0.55	0.72	0.90	0.88	0.93	0.91	0.90	0.93	0.64	0.91

4. Discussion

The genetic diversity of Daurian pikas in central Inner Mongolia was high, with highly polymorphic microsatellite loci. More than 50% of the burrow systems were occupied by non-kin, with the QG relatedness coefficient being negative, suggesting that the inhabitants of those burrow systems were less related in ancestry than the average [33], whereas social groups of Mongolian gerbils were kin-based (r > 0), with 36% of Mongolian gerbil social groups being first cousins (r = 0.125) and half-siblings (r = 0.25) [34]. Furthermore, our findings support the hypothesis that increases in genetic diversity reduce genetic relatedness in Daurian pikas but not in Mongolian gerbils. Therefore, the formation and dynamics of Daurian pika social groups may be different from those of Mongolian gerbils.

The Daurian pika population we genotyped exhibited stable survival probabilities and a slight decline in relative abundance from 2010 to 2012 [21]. The average expected heterozygosity ($H_e = 0.55-0.93$) of the microsatellite loci was higher ($H_e = 0.42-0.69$) than that of a declining population of American pikas (*O. princeps*) in Oregon, United States [35], and that ($H_e = 0.59-0.65$) of a fluctuating collared pika (*O. collaris*) population in Yukon, Canada [36]. Likewise, the genetic diversity of Daurian pika populations was higher than that of plateau pikas (*O. curzoniae*) in the Qinghai–Tibet Plateau, China [37]. Despite high genetic diversity, the observed heterozygosity of microsatellite loci tended to be lower than the expected heterozygosity, suggesting some level of inbreeding in Duarian pikas (Table 1). Daurian pika populations undergo frequent local extinctions, exhibiting dramatic population fluctuations [16]. For instance, Daurian pikas disappeared within a few hundred kilometers in our study regions after 2014 (G. Wang, personal observation). Daurian pika populations may maintain their high genetic diversity when a population colonizes a new habitat by mixing individuals of different genetic makeups.

Daurian pikas do not appear to excavate their burrow systems [11]. Daurian pikas outcompete Brandt's voles (*Lasiopodomys brandtii*) for space and often overtake the burrow systems of Brandt's voles [11]. Contrary to the kin-based composition of Mongolian gerbil

social groups, more than 50% of Daurian pika social groups (i.e., pikas inhibiting the same burrow system) consisted of non-kin group mates with negative QG relatedness coefficients. We propose two hypotheses to explain this observation. First, a family-based social group of Daurian pikas often consists of 3–4 Daurian pikas [38]. Daurian pikas from different family groups may colonize a burrow system to form a social group with high genetic diversity and low genetic relatedness (Figures 1a and 2a). This finding is consistent with the frequent local extinction and recolonization of Daurian pika populations in Inner Mongolia [16,21]. Octodon degus, a group-living rodent, also lacks a kin structure with lower genetic relatedness due to the high turnover of group members [39]. It is uncertain whether juvenile Daurian pikas delay their natal dispersal, which increases the genetic relatedness of social groups. Second, Daurian pikas that were captured in a burrow system over three years may belong to different families that successively colonized the same burrow system at different times. Similarly, different social groups of the group-living rodent tuco-tuco (*Ctenomys sociabilis*) occupy the same burrow systems in different years [40]. Therefore, the higher genetic diversity and lower genetic relatedness of Daurian pika social groups might be caused by the dispersal and recolonization of the same burrow systems by different family groups of different genetic makeups.

The genetic diversity of Mongolian gerbils on the typical steppe of Inner Mongolia ($H_e = 0.81$ –0.9, this study) is higher than that of wild populations in the periphery of its range ($H_e = 0.41$, Yinchuan, Ningxia, China; $H_e = 0.39$, Hohhot, Inner Mongolia, China) [41]. Mongolian gerbils have an ecological lifetime of 6–9 months, with most adults dying over winter [9,22,42]. The juvenile gerbils often disperse a short distance to gain reproductive opportunities and avoid inbreeding [6]. It is possible that a high genetic diversity of Mongolian gerbils is about 60–70 m, with genetic relatedness decreasing from 0.2 to 0.0 [43]. The distance between two burrow systems of Mongolian gerbils ranges from 18 m to 280 m [6]. Gray mouse lemurs (*Microcebus murinus*) form social or communal groups during the daytime [44]. The female lemurs have higher-than-average genetic relatedness, but they do not have any sign of inbreeding due to male dispersal [44]. The high genetic relatedness of Mongolian gerbil social groups is possibly caused by delayed dispersal or short-distanced dispersal, which is adequate to maintain the genetic diversity of social groups.

Daurian pikas are a keystone species on the Mongolian Plateau [45]. The Mongolian gerbil is a rodent species of economic and public health importance [14]. Our results demonstrate the high genetic diversity of both Daurian pikas and Mongolian gerbils and the potential effects of sociality on population genetic structure. However, future studies are needed to elucidate the mechanisms and roles of dispersal in the maintenance of the genetic diversity of the two species, which both exhibit frequent local extinctions and recolonizations.

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Institutional Review Board Statement: Our trapping and handling of Daurian pikas were approved by the Institutional Animal Use and Care Committee (IACUC) of the Institute of Zoology, the Chinese Academy of Sciences, and the Mississippi State University IACUC (protocol 11-031). Our trapping and handling of Mongolian gerbils were approved by the Institutional Animal Use and Care Committee of the Institute of Zoology, Chinese Academy of Sciences.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study will be openly available in a public repository after the manuscript is accepted for publication.

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