POPULATION STRUCTURE AND GENETIC DIVERSITY
OF SNOW LEOPARDS IN MONGOLIA AND IMPLICATIONS FOR CONSERVATION.

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Executive Summary

The endangered snow leopard occurs throughout Central Asia, however, its viability
remains poorly understood. Mongolia is an important range country, being the home to
the largest populations in the northern portion of its distribution. The landscape
connectivity among regions of this vast country has important conservation
implications. Dispersal can act as a buffer against mortality and enables natural re-
colonization. In contrast, small, isolated populations have higher extinction risks.
Therefore, it is important to determine if snow leopards occupying Mongolia consist of
several large metapopulations or a collection of smaller, isolated populations.

We used a noninvasive genetic approach to examine landscape connectivity of
snow leopards in Mongolia. During 2010 we sampled several areas by collecting scats
including Tsagaan Shuvuut and Turgen Strictly Protected Areas (SPA; Uvs Province), and
Khar Us Nuur National Park (NP), Munkhkhairkhan NP, and Altan Khokhii NP (Khovd
Province). We also conducted a collaborative survey with Russian biologists in the
Tsagaan Shuvuut SPA of Tuva Republic (Russia) and along Argut River in Altai Republic
(Russia), however, samples from Russia were not included in our analysis. We combined
scats collected in Mongolia with ones we previously obtained during surveys in the Gobi
Desert and Tsagaan Shuvuut for a total of 724 scats.

We extracted the DNA and used a snow leopard-specific panel for species, sex,
and individual identification and identified 239 snow leopards scats and a total of 57
individuals. Representative snow leopards (n = 43) were selected and genotyped at 19

microsatellite loci. The samples were divided into 6 subpopulations, 3 in the Gobi Desert including (1) Gurvansaikhan NP, (2) Bogd (Arts and Baga Bogd), (3) Tost (Tost Uul and Noyon Uul), and 3 in western Mongolia including (4) Jargalant (Khar Us Nuur NP), (5) Turgen SPA, and (6) Tsagaan Shuvuut SPA. The mean observed (H_o) was 0.457 and expected heterozygosity (H_e) was 0.617 and the number of alleles was 6.6.

A significant portion of population structure was explained by isolation-by-distance. The greatest genetic similarity was between Gurvansaikhan–Bogd and Tsagaan shuvuut–Turgen, which were also subpopulations geographically closest to each other. The highest differentiation tended to be between western–eastern pairs. The connectivity was more limited between Jargalant–Tsagaan shuvuut and Gurvansaikhan–Tost. The most divergent subpopulations were Gurvansaikhan/Bogd, Jargalant, and Tsagaan shuvuut.

In the east, population assignment and model-based clustering of individuals based on allele frequencies suggested movement between Tost and Gurvansaikhan/Bogd areas. However, Gurvansaikhan/Bogd also included individuals belonging to a genetic cluster not detected in any other areas. This suggests that there may be individuals dispersing into these sites from nearby un-sampled populations. In the west, Jargalant and Tsagaan shuvuut were the most divergent, and composed primarily of their own genetic clusters, while Turgen was a mix of clusters from the other 2 western subpopulations. Therefore Turgen may be part of a corridor that links adjacent areas.

Our study illustrates the utility of using samples collected during noninvasive genetic surveys for understanding population connectivity at a regional level, something that is not feasible with traditional approaches such as camera-trapping and telemetry. We provide the first estimates of genetic diversity of snow leopards based on samples from multiple populations and a preliminary look at structure and gene flow. Our analysis offers a foundation for snow leopard landscape genetics studies in Mongolia. We are sampling additional areas in 2011 to address some of the questions raised by our results.

Information on population connectivity generated from genetic studies such as this is important for understanding how landscape features affect snow leopard ecology, identifying large core populations, small isolated populations, and corridors that link areas. This knowledge is critical for predicting the effects of human actions, such as poaching and grazing of livestock, and developing effective conservation initiatives in Mongolia.

Objectives

The snow leopard is an endangered species whose populations are believed to be declining throughout Central Asia [1,2,3]. Mongolia covers a significant portion of the species range and harbors one of the largest snow leopard populations. Despite the information we have on the distribution and abundance of this species [4-11], the viability

of the snow leopard populations remains poorly understood. One important conservation question concerns the levels of connectivity among different populations.

When a species exhibits metapopulation dynamics, dispersal between areas acts as a buffer against higher mortality rates in subpopulations [12]. In addition, the re-colonization of sites where the species was recently extirpated naturally occurs in metapopulations. In contrast, when subpopulations are isolated the extinction risks are greatly increased, particularly when natural stochastic fluctuations are combined with anthropogenic stressors [12,13]. Therefore, it is important to determine if snow leopards occupying a region consist of a large metapopulation or a collection of smaller, isolated subpopulations [15,16].

Ecological data on snow leopard movement between isolated mountain ranges, frequency with which migrants successfully establish territories and breed, and overall population connectivity is not available in most regions because the traditional approach (i.e., telemetry) was and is being conducted in very few, small study sites because of logistical reasons [5,7,10]. Genetics can be leverage to address these questions at a regional level because genetic diversity provides information on population connectivity [15-19].

The purpose of our project was to understand landscape connectivity of snow leopards. We expected to contribute to knowledge by: (1) Generating abundance estimates by noninvasively genetic surveys in sites where quantitative data was not available. (2) Providing the first estimates of genetic diversity in Mongolia incorporating multiple populations. (3) Estimating the dispersal, levels of gene flow, and population structure within Mongolia. (4) Identifying mountain ranges, or regions, that act as metapopulation sources and those that act as sinks. (5) Establishing baseline information on population structure and diversity that in the future will be used to estimate effective population size and monitor long-term trends in snow leopard population dynamics. (6) Providing recommendations for management units and conservation priorities.

Methods

We collected snow leopard scats in the field, in 6 areas in Mongolia (Figure 1). Genetic analysis was conducted at Texas A&M University. The DNA was extracted from scat using the Qiagen Stool DNA extraction kit (Qiagen, Valencia, California, USA) and species, individual, and sex-identification was made using previously described protocols[20-25].

Individual identification was based on 4 loci (PUN100, PUN124, PUN225, PUN229; mean for 6 study sites $P_{ID-unrelated}$ = 0.0017, $P_{ID-sibs}$ = 0.055) [20,24,25]. Samples suspect of containing errors were either re-genotyped or discarded. Each snow leopard scat was initially genotyped in triplicate to minimize errors due to allelic dropout and false alleles[21,23].

Representative individuals were analyzed with 15 additional microsatellite loci developed by J. Janecka using previously described protocols [20]. Only samples successfully genotyped at all 4 microsatellite loci used for individual identification with

no errors were used for population structure analysis. Genetic parameters including allele numbers, observed heterozygosity (H_o), and expected heterozygosity (H_e), were estimated in GENALEX 6.41 [26,27]. Population structure was examined using several approaches. Differentiation between subpopulations was estimated using an F_{st} (GENALEX), Principal Coordinate Analysis (GENALEX), Mantel test for isolation-by-distance (GENALEX), population assignment (GENEALEX)[28], and model-based clustering (STRUCTURE) analysis[29].

Results & Discussion

Field Surveys

We collected more than 724 scats in Mongolia over the course of 4 years. From February to November 2010, we surveyed populations in Tsagaan Shuvuut and Turgen Strictly Protected Areas (SPA; Uvs Province), and Khar Us Nuur National Park (NP), Munkhkhairkhan NP, and Altan Khokhii NP (Khovd Province) from which in Turgen, of the 78 putative snow leopard samples collected, 34 were snow leopard (43.59%), in Tsagaan Shuvuut, 22 of 44 samples were scats of snow leopard, in Altan Khokhii, none of the 12 samples proved to be snow leopard. In September 2010, an additional 17 samples were collected in Turgen of which only 2 were snow leopard and Jargalant was surveyed with 62 scats collected (27 from snow leopard). The Tsagaan Shuvuut SPA is located along the border of Russia and Mongolia. A joint Mongolian-Russian field team surveyed Tsagaan shuvuut in Tuva (Russia) in February and Turgen and Tsagaan shuvuut SPA (Mongolia) in April 201. Scats from Russian Tsagaan shuvuut were sent to Moscow for analysis, results are not included in this report. There was no snow leopard scat and or sign registered along the middle part of Argut river in the Altai Republic, where the Russian –Mongolian joint team was working in November. The Jargalant Mountain is a part of Khar Us Nuur NP in Khovd province, western Mongolia, where a survey team collected snow leopard scats in 3 valleys. We were thinking that, the Jargalant and Altan Khokhii mountains are important corridors for snow leopards, linking populations in northern Altai and the main Altai mountain ranges. On 16 November 2010 in the Jargalant Mountains, Tseveenravdan, the director of Khovd branch of WWF-Mongolia Program Office, took about 600 pictures of a snow leopard on a kill site next to a livestock coral (personal comment) . The Munkhkhairkhan NP was surveyed for snow leopards for the first time, and contains excellent habitat in some of its valleys, although they are difficult to reach. During 6-days surveys in the Gurt valley we recorded 2 fresh snow leopard footprints, and found a carcass of an old snow leopard.

On 23-24 January 2011, the Munkhkhairkhan park director reported a snow leopard spent several hours (5:00-9:00 am) in the attic of a winter house located in a river valley southeast of Gurt (where we observed fresh footprints and found the dead snow leopard) valley. An old lady was alarmed by the cat and afraid to go out. The snow leopard ate some meat being prepared for the winter and dried for the spring and summer. Unfortunately, not many samples were found in the in Altan Khokhii NP partly because the weather was poor during survey time, with fresh snow covering most of the scats.

Genetic Variation
Representative individuals were selected from study sites (n = 43) and genotyped at 19 microsatellite loci. The samples were divided into 6 subpopulations; 3 in the Gobi Desert including (1) Gurvansaikhan NP, (2) Bogd (Arts and Baga Bogd), (3) Tost (Tost Uul and Noyon Uul), and 3 in western Mongolia including (4) Jargalant (Khar Us Nuur NP), (5) Turgen SPA, and (6) Tsagaan Shuvuut SPA. The mean allele's number per locus was 6.6. The H_e = 0.617 was higher than the H_o = 0.457, suggesting significant genetic structure (Table 1). Interestingly, the highest H_e was observed in Gurvansaikhan and Bogd (0.670 and 0.646), yet they had H_o similar to other areas (0.477 and 0.454). This could be explained in two ways, either these areas are mix of two divergent populations (i.e., lower H_o than expected because of two mixing populations, called the Wahlund effect) or genotyping errors. The samples used from these areas were selected based on the same rigorous criteria, and there was no evidence for genotyping error. Individuals from Gurvansaikhan and Bogd had private alleles not observed in any other subpopulation; suggesting that there may indeed be exchange with a divergent un-sampled population.

We examined levels of connectivity using several different approaches; F_{st} tests, Principle Coordinate Analysis, Mantel test of isolation-by-distance, population assignment, and model based clustering. The F_{st} estimates revealed significant differentiation among the western and eastern populations (F_{st} = 0.078, P = 0.001). In addition, pairwise F_{st} values were significant among all subpopulations except Gurvansaikhan–Bogd and Tsagaan shuvuut–Turgen. These were geographically closest to each other (155 km and 94 km, respectively). As could be predicted, the highest F_{st} values tended to be between pairs that included western–eastern subpopulations (Table 2). However, high F_{st} was also observed between Jargalant–Tsagaan shuvuut (368 km apart and F_{st} = 0.169), and between Gurvansaikhan–Tost (175 km apart and F_{st} = 0.115) suggesting more limited connectivity between these areas. The Mantel test found that significant portion of the genetic differentiation between areas was explained by geographic distance (P = 0.035; Figure 3). Principle Coordinate Analysis can visually reveal the structuring and relationship of populations. This analysis showed that that the most genetically similar subpopulations were Gurvansaikhan and Bogd, and the most divergent were Jargalant and Tsagaan shuvuut (Figure 4). Tost and Turgen shared the most variation with majority of the subpopulations.

Population assignment tests provide a more relevant estimation of current dispersal rates and can also be used to identify migrants (although our samples sizes were too small for this). In areas with higher migration, there will be a greater proportion of individuals assigned to subpopulations different from the ones in which they were sampled (termed "miss-assignments"). The population assignment results were somewhat contradictory with F_{st} estimates. Nearly 40% of individuals were miss-assigned, suggesting movement between the areas, although this could also be due to the limited samples size (Table 4).

Looking more closely at specific subpopulations; almost half of the individuals from Gurvansaikhan and Bogd were assigned to Tost, in contrast, Tost had no miss-assignments. This suggests movement from Tost into the other eastern areas, however, an absence of movement in the opposite direction. In western Mongolia, Turgen had

the greatest percentage of miss-assignments, suggesting that there is more frequent movement through this area, than in Jargaalnt and Tsagaan shuvuut. It is important to keep in mind that population assignment tests are strongly affected when there are source populations that have not been sampled. Therefore, additional sampling should be conducted in areas adjacent to our study sites to ensure confidence in population assignments.

Population structure tests can be biased by arbitrarily defining groups. There are models available that circumvent this problem by clustering individuals based on genetic variation, irrespective of sample origin. The Bayesian model found the most likely number of clusters in our dataset (i.e., cluster is synonymous with population) was 4 and their distribution suggested a more complex pattern of differentiation (Table 5; Figure 5).

In the east, Gurvansaikhan and Bogd were composed of individuals belonging to two genetic clusters; one occurring in only these two areas and the other primarily in Tost. It appears that there are indeed snow leopards in Gurvansaikhan/Bogd that do not share variation with Tost. These may come from a nearby by un-sampled population to the northwest in Bayantsagaan and Nemengt mountains. This is also supported by the higher H_e and greater number of individuals with private alleles in Gurvansaikhan/Bogd. Seven out of 15 individuals had multiple private alleles compared to only 1 out of 8 in Tost. In this region, the overall dispersal pattern appears to be higher from Tost to Gurvansaikhan/Bogd than in the reverse direction.

In the west, Jargalant was composed of only one genetic cluster, and individuals belonging to it were also observed in Turgen and Tsagaan shuvuut. Tsagaan shuvuut was primarily composed of its own cluster. However, Turgen was a mix of individuals belonging to the genetic clusters present in Tsagaan shuvuut and Jargalant. Because Turgen is composed of clusters from neighboring populations, it may be part of a corridor that links there areas. Consistent with this, there were no individuals observed in Turgen with private alleles.

Information on population connectivity generated from genetic studies incorporating samples collected during noninvasive surveys is important for understanding how landscape features affect snow leopard ecology and for identifying large core populations, small isolated populations, and corridors that link areas. This knowledge is critical for predicting the effects of human actions, such as poaching and grazing of livestock, and developing effective conservation initiatives in Mongolia. We are therefore working with the National Parks and Strictly Protected Areas of Mongolia, and NGOs such as WWF-Mongolia and Snow Leopard Conservancy, and local people to continue sampling in additional areas. We will work closely with government agencies in Mongolia to incorporate this information into conservation plans.

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Table 1. Genetic variation among snow leopard populations sampled in Mongolia.

LOCUS	GURVAN.			BOGD			TOST			JARGALANT		
	Na	Ho	He	Na	Ho	He	Na	Ho	He	Na	Ho	He
PUN82	8	0.778	0.840	4	0.667	0.694	2	0.875	0.492	3	0.667	0.542
PUN100	5	0.889	0.716	6	0.667	0.778	4	0.500	0.648	5	0.833	0.722
PUN124	5	0.556	0.784	8	1.000	0.847	4	1.000	0.680	4	0.667	0.625
PUN 132	4	0.222	0.593	2	0.000	0.444	1	0.000	0.000	2	0.167	0.153
PUN225	3	0.667	0.537	3	0.250	0.594	2	0.375	0.492	1	0.000	0.000
PUN229	7	0.444	0.747	6	0.667	0.778	4	0.375	0.539	4	0.500	0.694
PUN272	3	0.444	0.648	3	0.167	0.569	2	0.286	0.245	3	0.600	0.540
PUN327	4	0.143	0.663	5	0.600	0.780	3	0.375	0.320	3	0.167	0.486
PUN834	5	0.333	0.679	3	0.333	0.569	3	0.250	0.539	3	0.500	0.403
PUN894	4	0.667	0.741	4	0.500	0.597	3	0.750	0.664	3	0.833	0.625
PUN1131	6	0.444	0.753	6	0.400	0.800	3	0.375	0.398	2	0.167	0.153
PUN1139	3	0.222	0.537	4	0.600	0.740	3	0.500	0.461	2	0.167	0.153
PUN1157	5	0.556	0.710	4	0.400	0.700	3	0.875	0.594	3	0.667	0.653
PUN1262	6	0.667	0.772	4	0.500	0.625	3	0.375	0.539	1	0.000	0.000
PUN1283	5	0.375	0.727	4	0.333	0.722	2	0.000	0.490	3	0.400	0.560
PUN1293	5	0.556	0.698	3	0.333	0.611	1	0.000	0.000	2	0.600	0.420
PUN8972	2	0.600	0.420	4	1.000	0.719	2	0.750	0.469	2	0.800	0.480
PUNHBB	3	0.286	0.571	1	0.000	0.000	1	0.000	0.000	3	0.167	0.542
PUNHBE	3	0.222	0.593	4	0.200	0.700	2	0.125	0.117	2	0.167	0.153
Mean	4.5	0.477	0.670	4.11	0.454	0.646	2.53	0.410	0.405	2.68	0.425	0.416

Table 1. Continued.

LOCUS	TURGEN			TSAGAAN			MONGOLIA		
	Na	Ho	He	Na	Ho	He	Na	Ho	He
PUN82	3	0.667	0.653	3	0.875	0.648	9	0.767	0.724
PUN100	5	1.000	0.764	3	0.875	0.648	9	0.791	0.803
PUN124	3	0.333	0.625	3	0.625	0.602	10	0.698	0.810
PUN 132	4	0.500	0.625	4	0.750	0.711	5	0.279	0.578
PUN225	3	0.500	0.569	4	0.750	0.711	5	0.463	0.591
PUN229	3	0.333	0.486	3	0.625	0.617	10	0.488	0.739
PUN272	4	0.500	0.597	4	1.000	0.684	5	0.500	0.624
PUN327	4	0.833	0.583	3	0.375	0.398	6	0.400	0.580
PUN834	3	1.000	0.653	3	0.375	0.570	5	0.442	0.715
PUN894	3	0.500	0.569	3	0.500	0.398	4	0.628	0.701
PUN1131	1	0.000	0.000	1	0.000	0.000	9	0.238	0.461
PUN1139	1	0.000	0.000	3	0.375	0.320	7	0.310	0.465
PUN1157	2	0.333	0.444	2	0.125	0.117	7	0.500	0.631
PUN1262	3	0.333	0.569	3	0.250	0.227	7	0.372	0.645
PUN1283	2	0.000	0.278	3	0.714	0.582	9	0.306	0.644
PUN1293	2	0.167	0.486	2	0.125	0.117	5	0.286	0.483
PUN8972	3	0.500	0.403	3	0.500	0.406	4	0.667	0.536
PUNHBB	4	0.600	0.700	2	0.667	0.444	4	0.286	0.488
PUNHBE	3	0.500	0.542	2	0.375	0.305	5	0.262	0.507
Mean	2.947	0.453	0.502	2.84	0.520	0.448	6.58	0.457	0.617

Table 2. Pair-wise F_{st} values and significance among 6 areas sampled.

Region	Populaiton 1	Population 2	Pairwise F_{st}	P- value
East	Gurvansaikhan	Bogd	0.000	0.402
West	Turgen	Tsagaan	0.042	0.057
East vs West	Tost	Turgen	0.077	0.009
West	Jargalant	Turgen	0.082	0.008
East	Bogd	Tost	0.092	0.001
East vs West	Gurvansaikhan	Turgen	0.094	0.012
East vs West	Bogd	Turgen	0.110	0.001
East vs West	Tost	Jargalant	0.113	0.001
East	Gurvansaikhan	Tost	0.115	0.001
East vs West	Tost	Tsagaan	0.129	0.001
East vs West	Gurvansaikhan	Jargalant	0.137	0.001
East vs West	Gurvansaikhan	Tsagaan	0.155	0.001
East vs West	Bogd	Jargalant	0.156	0.001
West	Jargalant	Tsagaan	0.169	0.001
East vs West	Bogd	Tsagaan	0.196	0.001

Table 3. Population assignment of individuals sampled in 6 areas.

Population	Overall Missasignments				Population Assignments of Individuals					
	Self Pop	Other Pop	Percent Missassigned		Gurvansaikhan	Bogd	Tost	Jargalant	Turgen	Tsagaan
Gurvansaikhan	5	4	44.4%		5	0	5	0	0	0
Bogd	0	6	100.0%		2	0	4	0	0	0
Tost	8	0	0.0%		0	0	8	0	0	0
Jargalant	5	1	16.7%		0	0	0	5	1	0
Turgen	2	4	66.7%		0	0	1	1	2	3
Tsagaan	7	1	12.5%		0	0	0	1	0	6
Total	27	16	37.2%		7	0	18	7	3	9

Table 4. Likelihood probabilities estimated in STRUCTURE for K = 1 through K = 5 genetic clusters present among snow leopards sampled in Mongolia.

Clusters	Log Likelihood	Pr(K/X)
1	-1925.55	0
2	-1578.6	0
3	-1493.9	0
4	-1451.3	1.000
5	-1483.2	0
6	-1724.95	0

Figure 1. Map of areas sampled by scat surveys.
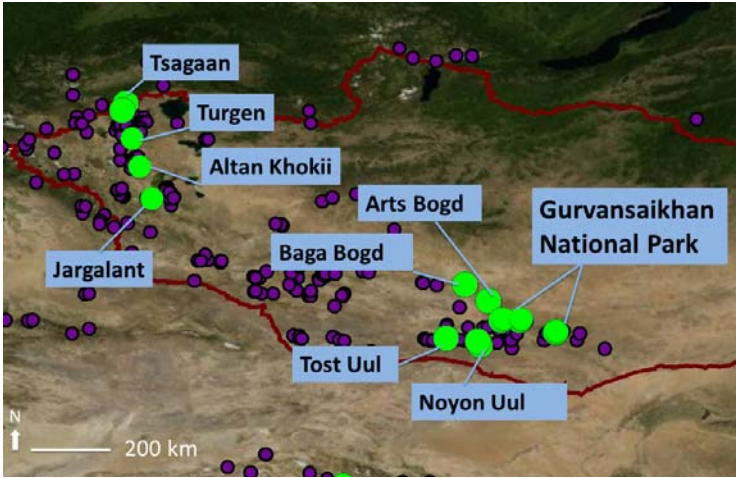
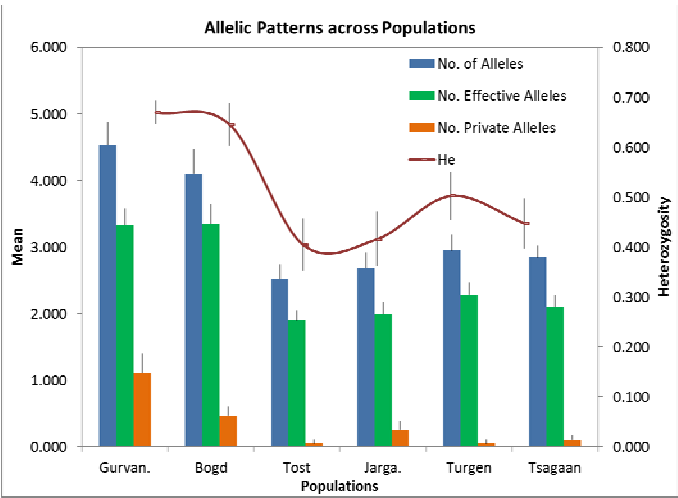

Figure 2. Patterns in allelic variation among snow leopards sampled in 6 areas of Mongolia.

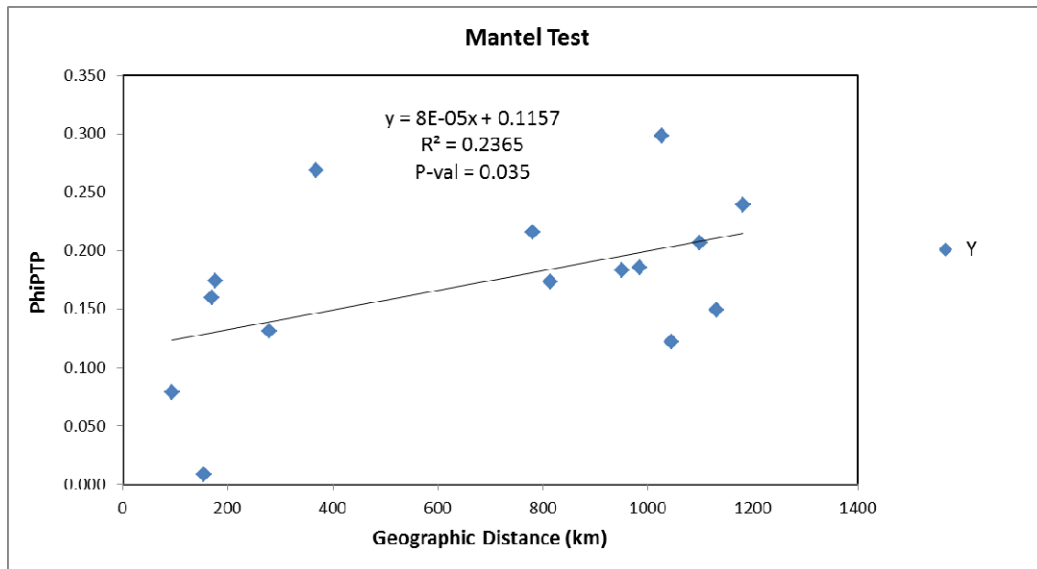Figure 3. Mantel test of isolation-by-distance for the 6 areas sampled in Mongolia.

Figure 4. Principle Coordinate Analysis of genetic variation among 6 areas sampled in Mongolia.
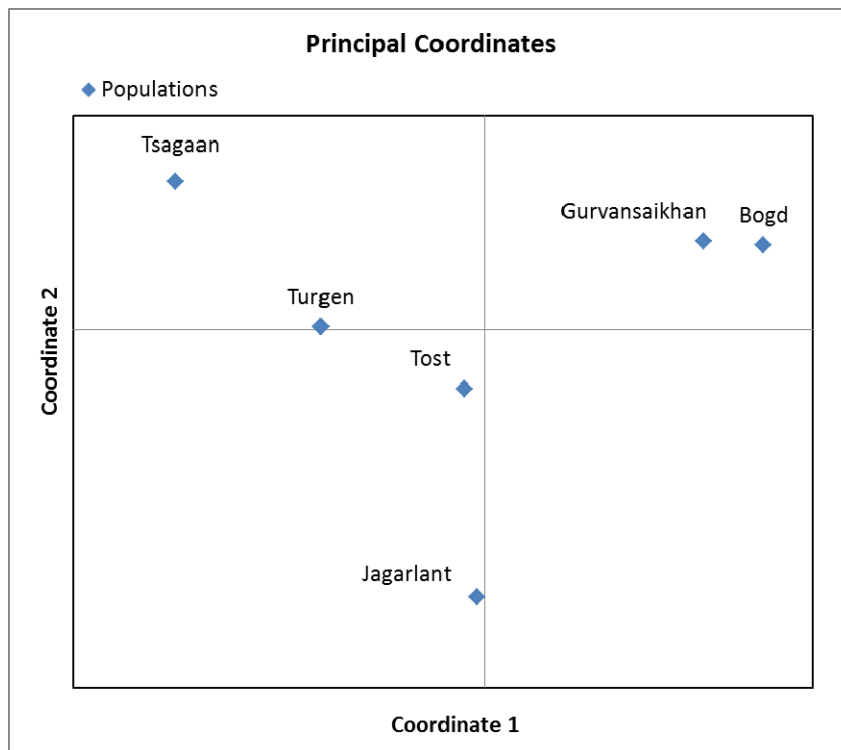
Figure 5. Four clusters identified in model-based analysis in STRUCTURE without regard for geographic origin and the distribution of individuals belonging to each cluster among sampled areas. Each color represents a unique cluster.
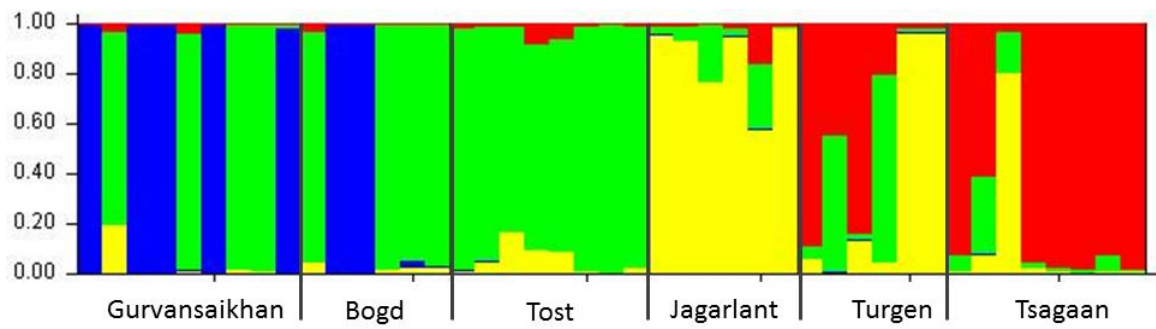

Photo 1. Survey team with local herders and park staff

Photo 2. Bariushaa Munkhtsog in the field

Photo 3. Snow leopard scat

Photo 4. Females of wild sheep-argali at study site

Photo 5. Local herders are moving to spring pasture from winter camp