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A karyotype comparison among 3 species of Allactaga (Mammalia: Dipodidae) from central Iran

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Abstract: We studied karyotype and chromosomal characteristics of 3 species of five-toed jerboa from central Iran, including *Allactaga firouzi*, *A. williamsi*, and *A. elater*. This study revealed that the 3 species possessed a diploid number of 48 chromosomes. The first pair of chromosomes was significantly larger than other chromosomes in all 3 species. The total length of the haploid genome of *Allactaga elater* was longer than those of the other 2 species, and most of the chromosomes of the 3 species were metacentric. Based on total form percentage, interchromosomal asymmetry index, and centromeric index, *Allactaga elater* had the highest interchromosomal asymmetry. *Allactaga firouzi* showed the highest between-chromosomal symmetry based on the difference of range of relative length, coefficient of variability, and intrachromosomal asymmetry index. Cluster analysis showed that *A. firouzi* and *A. williamsi* have more affinity than previously thought.

Key words: Dipodidae, *Allactaga firouzi*, *Allactaga elater*, *Allactaga williamsi*, karyotype, chromosomal characteristics, Isfahan

1. Introduction

Knowledge of the evolutionary history and genetic structure of species is necessary for conservation and management of biodiversity (Zhang et al., 2002; Mace et al., 2005).

Cytogenetic studies have long been used as an essential part of modern taxonomy and phylogenetics (Sybenga, 1992; Zima, 2000; Sheidai and Ghahremani-Nejad, 2008). Karyotype is determined by the number, size, and external shape of chromosomes and is considered a stable and definite characteristic of each species. Therefore, it can be indicative of the species and even genus, and it is useful in investigating the evolution of organisms and their classification (Hillis et al., 1996). Although numbers, morphology, and characteristics of chromosomes are different in most species, some closely related species have very similar karyotypes (Wurster and Benirschke, 1968).

Dipodids are a family of rodents adapted to desert and semidesert habitats. The family includes saltatorial species with very small forepaws and long legs and tail. The five-toed jerboas of genus *Allactaga* are distributed in arid and semidesert regions throughout northern Africa, the Iranian Plateau, and Central Asia to Mongolia. This genus has 12 species, of which 6 so far have been reported from Iran, including small five-toed jerboa (*Allactaga elater*), William's jerboa (*Allactaga williamsi*), Euphrates jerboa (*Allactaga euphratica*), Hotson's jerboa (*Allactaga hotsoni*), Iranian jerboa (*Allactaga firouzi*), and Toussi jerboa (*Allactaga toussi*) (Lay, 1967; Darvish et al., 2008; Tarahomi et al., 2010).

Allactaga firouzi was introduced as a new species by Womochel (1978); it is morphologically very similar to *A. hotsoni* (Thomas, 1920). This species was classified as Critically Endangered by the IUCN (1996) because of its restricted geographical distribution and habitat degradation. However, due to the lack of sufficient data on the population ecology of this species, its conservation status was changed to Data Deficient in 2008 (IUCN, 2012). *Allactaga williamsi* (Thomas, 1907) has been reported from West and Northwest Iran (Wilson and Reeder, 2005). The distribution range of this species extends to Turkey, Caucasia, Iran, and Afghanistan (Çolak et al., 1994; Ziaee, 1996). *Allactaga elater* (Gray, 1824) is the smallest and most common dipodid in Iran (Etemad, 1978). It is distributed throughout most of the desert and semidesert regions of Iran with the exception of the northern slope of the Alborz mountain forests. *Allactaga elater* also occurs in eastern Turkey, Central Asia, and Pakistan (Ziaee, 1996; Dianat et al., 2010).

Among the genus *Allactaga*, the karyotypes of 5 species including *A. elater*, *A. williamsi*, *A. euphratica*, *A. hotsoni*, and *A. toussi* have been previously reported (Çolak et al.,

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1994, 1997; Çolak and Yiğit, 1998; Darvish et al., 2006, 2008; Moradi Gharkheloo, 2009; Arslan and Zima, 2010; Aşan et al., 2010; Arslan et al., 2012; Moradi, 2013).

Low karyotype variability in the number of chromosomes has been documented; all 5 species possessed a diploid number of 48 chromosomes. However, the karyotype and chromosomal characteristics of *Allactaga firouzi* have yet to be investigated. The present study aimed to define karyotype and chromosomal characteristics of *A. firouzi* and to compare chromosomal characteristics of this species with *A. williamsi* and *A. elater* collected from Isfahan Province, central Iran.

2. Materials and methods

Three female specimens from 3 species of *Allactaga* including *Allactaga firouzi*, *A. williamsi*, and *A. elater* were captured from Isfahan Province, Iran. Ear biopsies were taken from the specimens and transferred to phosphate buffer saline without Ca^{2+} and Mg^{2+} (PBS^{-}) containing antifungal and antibiotics. Each sample tissue was cut up very finely and used for cell culture (Freshney, 1994). In brief, tissues were transferred into cell-culture flasks (T 25) containing Dulbecco's Modified Eagle Medium F/12 (DMEM/F12), supplemented with 15% fetal bovine serum] and placed in an incubator at 37 °C with 5% CO_2 and humidified air. After 1 week of culture, fibroblast cell monolayers had formed around the tissue explants. The explants were then removed, and the fibroblast cells were cultured to confluency (Freshney, 1994).

Chromosome counts were determined using standard preparation of metaphase spreads (Cooper et al., 1977). Cultured cells with a cell density of 80%–90% were treated with 0.1 µg of demecolcine and incubated at 37 °C for 1 h to obtain adequate numbers of cells in metaphase. The cells were then trypsinized briefly to separate dissected cells prior to cell fixing. Cells were then treated with hypotonic KCl buffer (0.075 M) for 15 min at 37 °C and fixed in Carnoy fixative solution (methanol/acetic acid; 3:1 v/v). The cell suspension was dropped onto clean slides and the chromosomes were stained with DAPI. Finally, the slides were observed and photographed with a fluorescent microscope (Olympus, BX51).

Photoshop software (Version 8) was used to open the captured pictures and prepare the karyotype. Idiograms of the species' chromosomes were prepared using Excel. Chromosome characteristics were measured in micrometers using MicroMeasure Version 3.3.

The chromosomal morphology was determined based on the arm ratio (Levan et al., 1964), where chromosomes were classified as metacentric (m), submetacentric (sm), subtelocentric (st), or acrocentric (a). The following features of chromosomes were evaluated: length of each chromosome (T), length of the long arm (L), length of the short arm (S), ratio of long arm to short arm (L/S), and centromeric index (CI = (S/L + S × 100). The detection of the homologous chromosomes and the determination of their positions in the karyotype were carried out according to Levan's method. Finally, the karyotypes of the 3 species were compared, and parameters including difference of range of relative length of largest and smallest chromosome (%DRL), total form percentage ($\%TF = \frac{\Sigma(S)}{\Sigma(T)} \times 100$), intrachromosomal asymmetry index ($A_1 = 1 - \frac{\sum_{i=1}^{n} (\frac{mean(S)}{mean(L)})}{n}$), interchromosomal asymmetry index ($A_2 = \frac{standart\ deviation(T)}{mean(T)}$), and coefficient of variability ($\%CV = A_2 \times 100$) were determined using the associated equations (Huziwara, 1962; Guerra, 1986; Romero Zarco, 1986).

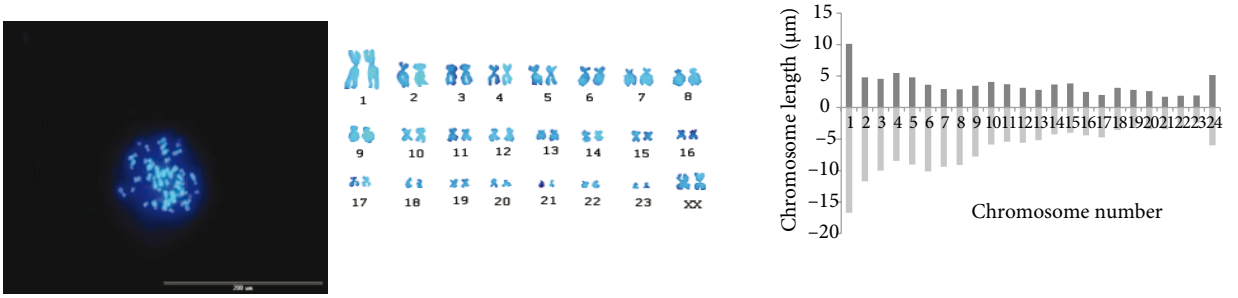
In the current study, statistical analyses including Pearson correlation coefficient and cluster analysis were conducted on chromosome characteristics of the 3 species using SPSS 18. The Pearson correlation coefficient was used to evaluate the type and intensity of correlation between karyotypes (Verma, 1980) and to compare the similarities or differences in chromosome characteristics. Pearson correlation coefficients for the 3 chromosome characters including the absolute length of chromosomes, length of short arms of chromosomes, and ratio of short arms to long arms of chromosomes were determined between the species. In addition, cluster analysis for grouping of the studied species based on their chromosome characteristics was performed using hierarchical cluster analysis with the middle method and squared Euclidean distance method.

3. Results

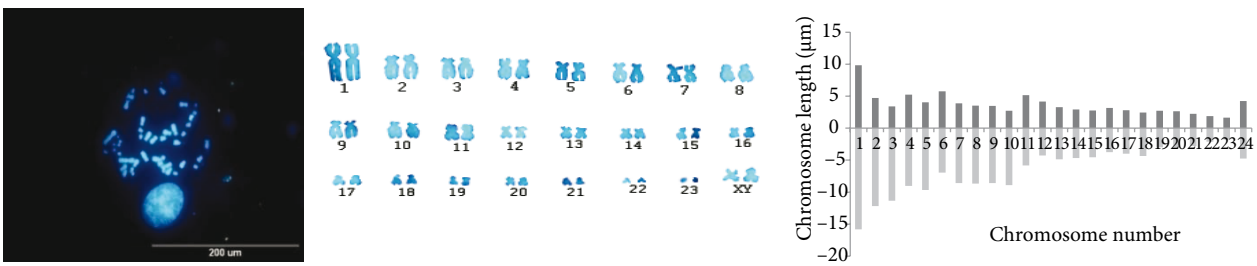
Cultured cells of *Allactaga firouzi*, *A. williamsi*, and *A. elater* were used for karyotyping and assessing their chromosomal characteristics. Karyotype images and diploid idiograms of the studied species are shown in Figure 1. All 3 species were diploid, and their karyotype was composed of 2n = 48 and FN = 96. Additionally, it was found that females had XX chromosomes. In all 3 species, the first pair of chromosomes was significantly larger than other chromosomes**.** All autosomes and X chromosomes were biarmed.

Chromosomal characteristics of the 3 *Allactaga* species were determined in micrometers using MicroMeasure 3.3 software (Table 1).

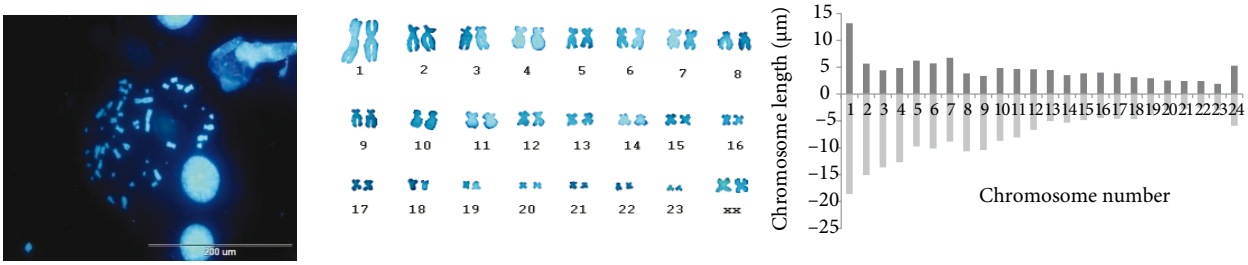
Allactaga firouzi: The karyotype formula of *A. firouzi* was 12 m + 10 sm + 2 st. The chromosome shapes of the 7th and 8th autosomes were subtelocentric, and other chromosomes were either metacentric or submetacentric. The X chromosome was of medium size and metacentric.



From left to right Mitotic metaphase chromosomes, Karyotype and Idiogram of *A. firouzi*



From left to right Mitotic metaphase chromosomes, Karyotype and Idiogram of *A. williamsi*



From left to right Mitotic metaphase chromosomes, Karyotype and Idiogram of *A. elater*

Figure 1. From left to right: metaphase chromosomes, karyotypes, and idiograms of *A. firouzi* (a), *A. williamsi* (b), and *A. elater* (c).

The first chromosome pair was metacentric and had absolute and relative lengths of 26.82 and 5.48 µm, respectively. The smallest chromosome was metacentric, with absolute and relative lengths of 4.35 and 0.89 µm, respectively (Table 1).

Allactaga williamsi: The karyotype formula of *A. williamsi* was 15 m + 7 sm + 2 st. The 3rd and 10th chromosomes were subtelocentric, but the other chromosomes were either metacentric or submetacentric. The X chromosomes were both medium-sized metacentrics. The first pair of chromosomes was the largest pair and metacentric. They had an absolute length of 25.65 µm; the relative length of these chromosomes was 5.30 µm. The absolute and relative lengths of the smallest chromosome, which was a metacentric chromosome, were calculated respectively at about 3.41 and 0.70 µm.

Allactaga elater: The karyotype formula of *A. elater* was 16 m + 6 sm + 2 st. The shape of the 3rd and 9th chromosomes was subtelocentric, and the other chromosomes were either metacentric or submetacentric. The X chromosome was metacentric, as in the other species, and was medium in size.

Table 1. Comparison of chromosomal characteristics of the 3 species studied. DRL: difference of range of relative length, CV: coefficient of variation, TF: total form percentage, A_1: intrachromosomal asymmetry index, and A_2: interchromosomal asymmetry index.

Species			Chromosomal characteristics
Allactaga elater	*Allactaga williamsi*	*Allactaga firouzi*	
16 m + 6 sm + 2 st	15 m + 7 sm + 2 st	12 m + 10 sm + 2 st	Karyotype formula
31.76	25.65	26.82	Absolute length of the largest chromosome (μm)
5.45	5.30	5.48	Relative length of the largest chromosome
4.87	3.41	4.35	Absolute length of the smallest chromosome (μm)
0.83	0.70	0.89	Relative length of the smallest chromosome
583.28	484.16	488.98	Total length of haploid genome (μm)
183.28	153.29	156.84	Total length of long arms (μm)
108.39	88.75	87.62	Total length of short arms (μm)
12.15	10.09	10.19	Average absolute length of chromosomes (μm)
2.08	2.08	2.08	Average relative length of chromosomes
7.61	6.39	6.53	Average length of long arms (μm)
4.52	3.70	3.65	Average length of short arms (μm)
1.70	1.72	1.82	Average ratio of long arms to short arms
0.66	0.66	0.61	Average ratio of short arms to long arms
39.01	38.82	37.08	Average centromeric index (CI)
2C	2C	2C	Karyotype classifications following Stebbins's method
4.62	4.60	4.59	DRL (%)
50.08	49.11	48.51	CV (%)
37.17	36.66	35.84	TF (%)
0.34	0.34	0.39	A_1
0.51	0.49	0.48	A_2

3.1. Pearson correlation

Results of Pearson correlation analysis are presented in Table 2. The correlation coefficients for the absolute lengths of chromosomes between the 3 species were more than 0.985 and all coefficients were significant ($P < 0.01$); therefore, it was shown that the absolute lengths of chromosomes were homogenous for the 3 species (Table 2).

Despite the significance of all correlation coefficients for length of short arms, these coefficients were smaller compared to correlation coefficients of absolute length of chromosomes (Table 2). Correlation coefficients for ratio of short arms to long arms in most cases were not significant; only the coefficient between *Allactaga elater* and *A. williamsi* was significant ($P < 0.01$) (Table 2).

3.2. Cluster analysis

The obtained dendrogram based on cluster analysis showed that these 3 species consisted of 2 distinct clusters. One cluster incorporated *A. firouzi* and *A. williamsi*, but *A. elater* was placed in a separate cluster, suggesting that *A. firouzi* and *A. williamsi* were closely related based on chromosomal characters (Figure 2).

4. Discussion

In this study, we determined the karyotype of *Allactaga firouzi* for the first time and compared the chromosomal characteristics of the species with those of *A. williamsi* and *A. elater*. We found that, like other species of the genus *Allactaga*, *A. firouzi* had 48 chromosomes (2n = 48) and the total number of chromosome arms equaled 96 (NF = 96).

Table 2. Pearson correlation (coefficients, significance, and degrees of freedom) for absolute length of chromosomes, length of short arms of chromosomes, and ratio of short arms to long arms of chromosomes for *A. firouzi*, *A. williamsi*, and *A. elater*.

Character		Ratio of short arms to long arms of chromosomes			Length of short arms of chromosomes			Absolute length of chromosomes		
Species		*A. firouzi*	*A. williamsi*	*A. elater*	*A. firouzi*	*A. williamsi*	*A. elater*	*A. firouzi*	*A. williamsi*	*A. elater*
	Coefficient	1.000	0.985	0.988	1.000	0.869	0.877	1.000	0.369	0.335
A. firouzi	Significance	-	0.000	0.000	-	0.000	0.000	-	0.000	0.000
	df	0	22	22	0	22	22	0	22	22
	Coefficient	0.985	1.000	0.996	0.869	1.000	0.913	0.369	1.000	0.626
A. williamsi	Significance	0.000	-	0.000	0.000	-	0.000	0.076	-	0.001
	df	22	0	22	22	0	22	22	0	22
	Coefficient	0.988	0.996	1.000	0.877	0.913	1.000	0.335	0.626	1.000
A. elater	Significance	0.000	0.000	-	0.000	0.000	-	0.110	0.001	-
	df	22	22	0	22	22	0	22	22	0

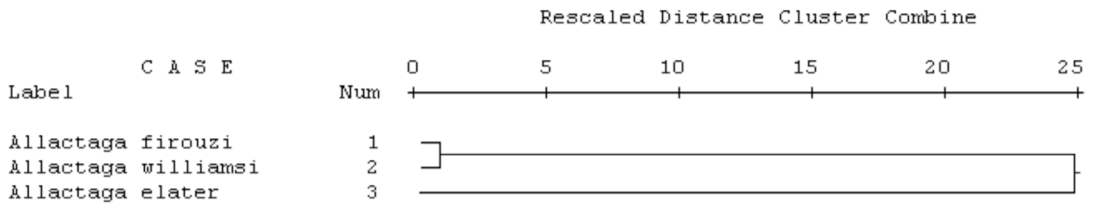


Figure 2. Dendrogram of the 3 *Allactaga* species based on chromosomal characters, using cluster analysis.

The number of chromosomes and number of chromosome arms of *A. elater* (Çolak et al., 1997), *A. euphratica* (Çolak et al., 1997; Çolak and Yiğit, 1998; Moradi Gharkheloo, 2009; Arslan et al., 2012), *A. hotsoni* (Darvish et al., 2006), *A. toussi* (Darvish et al., 2008), and *A. williamsi* (Arslan and Zima, 2010; Aşan et al., 2010) have respectively been reported as 2n = 48 and NF = 96. Zima (2000) and Shahin and Ata (2004) previously reported that the genus *Allactaga* had low karyotype variability, especially in diploid number of chromosomes. This karyotypic uniformity at the generic level has several reasons, including the phylogenetic age of this taxon, population dynamics, and population structure.

Number of chromosomes has been correlated with ecological conditions. In mole rats, for example, Nevo et al. (1995) indicated that the number of chromosomes increases with aridity. All specimens in the current study were captured in Isfahan Province under similar climatic conditions (annual rainfall and humidity). Nevertheless, some ecological peculiarities exist among the habitats of the 3 species. *Allactaga firouzi* lives in semiarid lands with a high percentage of bare soil and the *Anabasis* type of vegetation (Naderi et al., 2009), *A. elater* lives in salty semiarid areas with various kinds of halophytes, and the favorable habitat for *A. williamsi* is steppe areas with sparse vegetation.

Çolak et al. (1994) found 1 subtelocentric, 15 submetacentric, and 7 metacentric pairs in the chromosome set of *A. williamsi*. Aşan et al. (2010) reported 14 submetacentric, 6 metacentric, and 3 subtelocentric pairs in *A. williamsi*. Arslan and Zima (2010) stated that in the chromosome set of *A. williamsi*, there were 12 submetacentric, 7 metacentric, and 5 subtelomeric pairs. Moradi (2013) also noted 15 submetacentric, 1 subtelocentric, and 7 metacentric pairs in the Iranian specimens of *A. williamsi*, and 14 submetacentric, 5 subtelocentric, and 4 metacentric pairs in *A. elater*. In the current study, we determined 15 metacentric, 7 submetacentric, and 2 subtelocentric pairs in *A. williamsi*; 16 metacentric, 6 submetacentric, and 2 subtelocentric pairs in *A. elater*; and 12 metacentric, 10 submetacentric, and 2 subtelocentric pairs in *A. firouzi*. Different methods used for classification of the chromosomes by the authors might be the reason for the dissimilarities between the data.

All 3 species studied were placed in the 2C class of Stebbins's (1971) method, indicating the presence of asymmetrical karyotypes in the length of their chromosomes; however, the locations of the centromeres were relatively symmetric.

Intrachromosomal asymmetry was determined based on TF, A_1, and centromeric index. The results show that *A. elater* has maximum TF, average centromeric index, and minimum A_1. Minimum TF, average centromeric index, and maximum A_1 were obtained for *A. firouzi*. Therefore, *A. elater* possessed the most symmetrical and *A. firouzi* the most asymmetrical karyotypes. The karyotypic formula of the species confirms the above conclusions. Based on karyotypic formula, *A. elater* and *A. firouzi* had 16 and 12 metacentric chromosomes respectively, indicating that the symmetry of the intrachromosome for *A. elater* was larger. Interchromosomal symmetry was examined using CV, DRL, and A_2. Based on the results, the lowest DRL, CV, and A_2 were obtained for *A. firouzi*; the highest values of these indicators belonged to *A. elater*. Thus, the maximum and minimum intrachromosomal symmetry existed in *A. firouzi* and *A. elater*, respectively. We used different indices for inter- and intrachromosomal asymmetry and obtained concordant results. Therefore, it can be suggested that A1 and A2 indices, which originally were developed and calculated in higher plants (Stebbins, 1971), can be used in other species, such as those of the class Mammalia. The above indices have been used for chromosomal asymmetry of other animal species such as snails, as stated by Diupotex-Chong et al. (2007).

The Pearson correlation coefficients demonstrated that the absolute lengths of chromosomes among the 3 species were homogeneous, while the length of short arms and ratio of short arms to long arms were heterogeneous. The existence of a very high Pearson correlation coefficient for absolute length of chromosome and low correlation for length of short arms and ratio of short arms to long arms in these 3 species can be considered as an indicator of structural changes in chromosomes. In other words, with the stability of length of chromosomes in these 3 species, structural changes of chromosomes may have occurred by displacement of the centromeres (Table 2). However, chromosomal banding including G- and C-banding is required for confirmation. Previously, Çolak et al. (1994) showed that *A. euphratica* and *A. williamsi* differed in the location of the centromere of the first chromosome pair. In *A. euphratica*, the centromere was located centrally, while in *A. williamsi* it was located peripherally. In this study, the first pair of chromosomes in all 3 species was metacentric and clearly larger than the other chromosomes.

Cluster analysis based on chromosomal characteristics showed that *A. firouzi* and *A. williamsi* had more affinity than previously thought (Figure 2). Tarahomi et al. (2010) showed that, based on skull morphometrics, *A. williamsi* was a greater distance from the other species and *A. firouzi* and *A. elater* were closely related. Other studies based on morphometric (Shenbrot, 2009) and molecular (Dianat et al., 2010) data showed that the Iranian jerboa and Hotson's jerboa belong to a single species. This emphasizes the importance of chromosomal studies for better understanding of the taxonomic status of the *Allactaga* genus, especially for *A. firouzi*. G- and C-banding are recommended to provide more insights into phylogenetic and taxonomic relationships and to confirm the species status of *A. firouzi*. Banding studies could reveal the level of chromosomal divergence and chromosomal differences between the 2 potentially synonymous species, *A. hotsoni* and *A. firouzi*, in such a way that the combined data will provide sufficient information for a proper assessment of conservation status of the species. Unresolved taxonomic issues hinder the effective management of the species. Iranian jerboa has a very restricted distribution with a low population size and density in Shahreza, Isfahan. The dominant process that threatens the species is habitat degradation due to the grazing of domesticated sheep and goats (Naderi et al., 2009). Therefore, it is necessary to establish a protected area in the region with restricted access for villagers and to monitor the species' population.

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