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Morphological and demographic characteristics of the grey hamster (Nothocricetulus migratorius) across lowland and foothill landscapes of the South Caucasus

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Abstract

The grey hamster, *Nothocricetulus migratorius* (Pallas, 1773), is widely distributed across Eurasia, but information on its morphology, demographic structure, and long-term population patterns in the South Caucasus remains limited. We analysed data from lowland and foothill landscapes of the Martuni region, Nagorno-Karabakh, collected during 1999–2023, together with comparative observations from Artashat and Armavir, Armenia, during 2024–2025. A total of 540 surveys corresponding to 54,000 trap placements yielded 13,869 small mammals, including 1,730 grey hamsters. Of all trap placements, 37,972 represented active trap-days and were used to standardize relative abundance. Relative abundance averaged 4.82 individuals per 100 active trap-days in the lowland zone and 4.42 in the foothill zone. In the Armenian sample, it was 2.73 individuals per 100 active trap-days. Long-term observations in Nagorno-Karabakh revealed substantial interannual variation, with lower relative-abundance values during the later years of monitoring. Morphometric variation was trait-specific rather than uniform across geographic groups. Body length was greater in foothill than in lowland animals, whereas tail length, hind-foot length, and zygomatic width were generally greater in lowland animals. The Armenian sample showed comparatively high mean values for several external and cranial measurements. Age structure also varied among localities. These results demonstrate substantial spatial, temporal, morphometric, and demographic variation in *N. migratorius* and provide a baseline for continued standardized monitoring in the South Caucasus.

Introduction

Small mammals are important components of terrestrial ecosystems, where they contribute to trophic interactions, seed and plant material consumption, soil processes, and food-web dynamics. At the same time, many rodent populations show pronounced spatial and temporal fluctuations in abundance, which may be associated with variation in food resources, vegetation structure, climatic conditions, predation, reproduction, and habitat disturbance (Krebs 1974, 1996; Dickman 1999). Long-term monitoring is therefore particularly important for distinguishing short-term fluctuations from persistent changes in rodent populations.

The grey hamster, *Nothocricetulus migratorius* (Pallas, 1773), is a small cricetid rodent with a broad Palearctic distribution extending from southeastern Europe through the Caucasus and the Middle East to Central Asia, Mongolia, and western China (Gromov and Erbajeva 1995; Kryštufek et al. 2008; Kryštufek and Vohralík 2009). The species occupies a wide variety of environments, including steppes, semi-deserts, agricultural landscapes, and habitats associated with human settlements, and occurs across a broad elevational range (Gromov and Erbajeva 1995; Kryštufek and Vohralík 2009; Nedyalkov 2016) .

The species was traditionally classified as *Cricetulus migratorius*. However, molecular phylogenetic analyses demonstrated that *Cricetulus* in its former broad sense was polyphyletic and that the grey hamster is phylogenetically more closely related to *Cricetus* and *Allocricetulus* than to *Cricetulus* sensu stricto. Consequently, Lebedev et al. (2018) established the new genus *Nothocricetulus* for the grey hamster. Accordingly, the currently accepted name *Nothocricetulus migratorius* is used throughout the present study (Lebedev et al. 2018) .

Despite its broad geographic distribution and ecological flexibility, the abundance and population status of the grey hamster can vary substantially among regions. In Bulgaria, for example, recent investigations documented a marked contraction of its known distribution, with contemporary records concentrated in the southeastern part of the country (Nedyalkov, 2016). Such regional differences emphasize that a species with a broad overall distribution may nevertheless show pronounced local variation in occurrence and abundance.

The South Caucasus forms an important part of the distribution range of the grey hamster. The species has long been recorded in Armenia and adjacent parts of the Caucasus (Sosnikhina, 1950; Dal, 1954; Gromov & Erbajeva, 1995; Yavruyan & Hayrapetyan, 2003; Bukhnıkashvili, 2004). Earlier studies from Armenia and Nagorno-Karabakh provided information on its occurrence, ecology, and association with natural and human-modified habitats (Sosnikhina, 1950; Yavruyan & Hayrapetyan, 2003; Hayrapetyan, 2012, 2014). These regional studies constitute an important historical baseline, but long-term quantitative information on temporal changes in abundance remains comparatively limited.

Recent long-term research in the Martakert and Varnkatagh communities of Nagorno-Karabakh demonstrated substantial temporal and spatial variation in grey hamster populations during 1999–2023 (Hayrapetyan et al., 2025). These findings highlighted the importance of extended monitoring for understanding population dynamics of the species in the South Caucasus. However, the Martakert–Varnkatagh dataset represents a geographically distinct study system and does not replace the need for independent assessment of populations in other parts of the region.

Population abundance alone may not fully characterize geographic variation in a species. Morphometric characteristics and demographic structure provide complementary information because body dimensions, cranial measurements, sex composition, and age structure may differ among populations and sampling periods. Previous studies have documented considerable geographic and morphometric variability in the grey hamster across its range (Gromov & Erbajeva, 1995; Kryštufek & Vohralík, 2009; Nedyalkov, 2016). Examining such characteristics together with standardized abundance data may therefore provide a more complete description of population variation.

The present study analyzes long-term data on *N. migratorius* from the Martuni region of Nagorno-Karabakh collected during 1999–2023 and complementary observations from Artashat and Armavir in the Republic of Armenia collected during 2024–2025. Unlike the previously published Martakert–Varnkatagh dataset (Hayrapetyan et al., 2025), the present study focuses on an independent set of localities and additionally evaluates geographic variation in morphometric and demographic characteristics.

The objectives of the present study were to: (1) evaluate long-term temporal variation in the relative abundance of *N. migratorius* in the Martuni region; (2) compare capture-based relative abundance among lowland and foothill landscapes and individual localities using effective trapping effort; (3) describe and compare morphometric characteristics among the studied geographic groups and between sexes; and (4) characterize the sex and age structure of the sampled populations. By integrating long-term trapping records with morphometric and demographic observations, the study provides a standardized baseline for further monitoring of *N. migratorius* populations in the South Caucasus.

Materials and Methods

Study area

Field investigations were conducted in lowland and foothill landscapes of the Martuni region, Nagorno-Karabakh, from 1999 to 2023. Six localities were included in the long-term study: Martuni, Kakavadzor, and Kajavan in the lowland zone, and Berdashen, Ashan, and Gishi in the foothill zone. Additional observations were conducted in Artashat and Armavir in the Republic of Armenia during 2024–2025. The locations of the study sites are shown in Fig. 1.

[Insert Fig. 1 here]

The lowland localities differed in elevation and climatic characteristics. Martuni (39°47'43" N, 47°06'40" E) was situated at 400 m a.s.l. and was characterized by a dry subtropical climate, with an average annual temperature of 14–15°C and annual precipitation of approximately 300–350 mm. Kakavadzor (39°50'09" N, 47°09'42" E) was located at 265–300 m a.s.l., with a dry subtropical climate, an average annual temperature of 16–17°C, and annual precipitation of approximately 250–300 mm. Kajavan (39°45'50" N, 46°54'43" E) was located at 400–450 m a.s.l. and was characterized by a temperate, warm, dry climate, with an average annual temperature of 10–12°C and annual precipitation of approximately 400–500 mm.

The foothill localities were situated at higher elevations. Berdashen (39°50'51" N, 47°01'49" E) was located at 750–800 m a.s.l. and was characterized by a temperate, warm, humid climate, with annual precipitation of approximately 700–750 mm. Ashan (39°50'47" N, 46°59'49" E) was located at 700–750 m a.s.l., with annual precipitation of approximately 650–700 mm, whereas Gishi (39°46'31" N, 47°01'13" E) was located at 650–700 m a.s.l., with annual precipitation of approximately 600–650 mm.

For geographic comparison, observations were also conducted in the Ararat Valley of the Republic of Armenia. The Artashat study site (39°57'14" N, 44°33'02" E) was located at 900–1050 m a.s.l., and the Armavir study site at 890–950 m a.s.l.

Elevation and geographic coordinates were determined in the field using a Garmin GPSMAP 64s.

Trapping design and field sampling

The animals examined in this study originated from two sources. Field material consisted of wild grey hamsters (Nothocricetulus migratorius) captured during long-term small-mammal surveys conducted in the Martuni region of Nagorno-Karabakh from 1999 to 2023 and during additional field surveys in Artashat and Armavir, Republic of Armenia, in 2024–2025. In addition, specimens from the scientific collection of the Scientific Center of Zoology and Hydroecology, National Academy of Sciences of the Republic of Armenia, were used for comparative morphometric analyses. No privately owned, farm, or companion animals were used in the study.

Small mammals were surveyed using live traps. Traps were deployed at a nominal density of 100 traps per survey day within a 1-ha sampling area and were arranged in a checkerboard pattern at approximately 10 × 10 m spacing. Traps were checked three to four times per day. The bait consisted of carrots and bread soaked in oil; fat or sausage was occasionally used. Additional details of the trapping procedure have been described by Hayrapetyan et al. (2025).

A total of 540 surveys were conducted during the entire study period, including 18 surveys in the Republic of Armenia during 2024–2025. These surveys corresponded to 54,000 trap placements. Because not all deployed traps remained functional, total trap placements were distinguished from effective trapping effort. Of the 54,000 trap placements, 37,972 were recorded as active and 16,028 as inactive (Table 1).

Only active traps were used as the denominator for calculations of relative abundance. Relative abundance of the grey hamster was calculated as:

Relative abundance = (number of Nothocricetulus migratorius captured / number of active trap-days) × 100.

Accordingly, relative abundance is reported throughout the study as the number of grey hamsters captured per 100 active trap-days rather than per 100 total trap placements.

Across all study sites and years, 13,869 small mammals were captured, of which 1,730 were identified as *N. migratorius*. Annual trapping effort and numbers of captured animals are presented in Table 1, whereas the distribution of trapping effort and grey hamster captures among landscape zones and individual localities is presented in Table 2.

Species identification and nomenclature

Grey hamsters were identified on the basis of external morphological characteristics using regional mammalian identification keys and reference works (Vinogradov & Gromov, 1984; Pavlinov et al., 2002; Yavruyan & Hayrapetyan, 2003).

The species was historically referred to as *Cricetulus migratorius*. Molecular phylogenetic analyses subsequently demonstrated that *Cricetulus* in its traditional broad sense was polyphyletic, and Lebedev et al. (2018) established the genus *Nothocricetulus* for the grey hamster. Accordingly, the species is treated here as *Nothocricetulus migratorius* (Pallas, 1773), and this nomenclature is used consistently throughout the manuscript.

Morphometric measurements

Morphometric measurements were obtained from grey hamsters captured in the lowland and foothill zones of Nagorno-Karabakh and from the study sites in the Republic of Armenia.

Linear measurements were taken using an electronic caliper with a precision of 0.01 mm, and body mass was measured using electronic scales with a precision of 0.01 g.

The following external and cranial measurements were recorded: body length (BL), tail length (TL), hind-foot length (HFL), ear length (EL), skull length (SL), zygomatic width (ZW), interorbital width (IOW), nasal length (NL), nasal width (NW), and body mass (g).

Sample size differed among measurements. External measurements and body mass were available for 109 males and 114 females from the lowland zone, 123 males and 113 females from the foothill zone, and 17 males and 20 females from the Republic of Armenia. Cranial measurements were available for smaller subsets of animals; therefore, the exact sample size (*n*) for each sex, geographic group, and morphometric trait is reported separately in Table 3.

For each morphometric variable, descriptive statistics were calculated separately by sex and geographic group and are presented as sample size (*n*), minimum–maximum range, arithmetic mean (M), standard error of the mean (m), and standard deviation (SD).

Age determination

Age classification was based on a combination of external morphology and dental characteristics. General procedures for age differentiation in small rodents followed methodological approaches described by Bashenina (1953), Koshkina (1955), Larina and Lapshov (1974), Tupikova et al. (1970), and Klevezal (2007). These references were developed primarily for arvicoline rodents and were therefore used as methodological guidance rather than as species-specific age standards for *N. migratorius*.

Dental assessment included examination of molar development and crown wear. Dental surfaces were examined using an MBS-10 binocular microscope at 7× magnification, and measurements, where required, were made using an electronic caliper with a precision of 0.01 mm.

On the basis of the combined morphological and dental assessment used in the field protocol, individuals were assigned to three demographic categories: juvenile (Juv), subadult (Sad), and adult (Ad). These categories were subsequently used to describe demographic structure among the studied localities.

Statistical analysis

Statistical analyses were performed using IBM SPSS Statistics, version 27.

Descriptive statistics for morphometric variables included sample size (*n*), arithmetic mean (M), standard error of the mean (m), standard deviation (SD), and minimum–maximum values. Morphometric characteristics were summarized separately for males and females and for the lowland, foothill, and Armenian samples.

Relative abundance was standardized according to effective trapping effort and expressed as the number of *N. migratorius* captured per 100 active trap-days. Active rather than total trap placements were used in these calculations to account for traps recorded as non-functional during sampling.

Annual and locality-specific values of relative abundance were summarized and compared descriptively; no inferential statistical tests were applied to temporal or spatial differences in relative abundance.

Because sample sizes differed among morphometric variables, particularly between external and cranial measurements, descriptive summaries were based on the available observations for each individual trait rather than assuming a common morphometric sample size across all variables.

Results

Overall trapping results and temporal variation

During the entire study period, 540 surveys were conducted, corresponding to 54,000 trap placements. Of these, 37,972 were active and 16,028 were recorded as inactive. A total of 13,869 small mammals were captured, including 1,730 grey hamsters (*Nothocricetulus migratorius*).

Using only active traps as the measure of effective trapping effort, the overall relative abundance of *N. migratorius* was **4.56 individuals per 100 active trap-days** (1,730 individuals/37,972 active trap-days × 100).

Annual trapping effort and capture data are presented in Table 1. Relative abundance was calculated for each year using the number of active trap-days rather than the total number of traps deployed.

Table 1. Number of traps set and animals captured in different years

Year	Number of surveys	Total traps	Active traps	Inactive traps	Number of animals captured	of which, grey hamsters	Grey hamsters per 100 active trap-days
1999	24	2,400	1,785	615	719	111	**6.22**
2000	25	2,500	1,889	611	736	111	**5.88**
2001	21	2,100	1,539	571	607	83	**5.39**
2002	22	2,200	1,572	618	554	74	**4.71**
2003	22	2,200	1,557	633	606	80	**5.14**
2004	24	2,400	1,678	722	603	73	**4.35**
2005	22	2,200	1,572	628	573	77	**4.90**
2006	23	2,300	1,614	686	599	73	**4.52**
2007	21	2,100	1,414	696	526	69	**4.88**
2008	23	2,300	1,637	663	616	84	**5.13**
2009	22	2,200	1,569	631	562	69	**4.40**
2010	23	2,300	1,490	810	520	75	**5.03**
2011	23	2,300	1,607	693	559	74	**4.60**
2012	24	2,400	1,698	702	630	78	**4.59**
2013	24	2,400	1,654	746	589	70	**4.23**
2014	23	2,300	1,655	645	637	75	**4.53**
2015	24	2,400	1,676	724	576	72	**4.30**
2016	21	2,100	1,427	673	483	60	**4.20**
2017	24	2,400	1,645	755	577	63	**3.83**
2018	22	2,200	1,552	648	567	60	**3.87**
2019	24	2,400	1,591	809	477	56	**3.52**
2020	12	1,200	800	400	277	30	**3.75**
2021	13	1,300	879	421	300	33	**3.75**
2022	10	1,000	714	286	271	27	**3.78**
2023	6	600	403	197	140	16	**3.97**
2024	9	900	662	238	275	16	**2.42**
2025	9	900	693	207	290	21	**3.03**
Total	**540**	**54,000**	**37,972**	**16,028**	**13,869**	**1,730**	**4.56**

Relative abundance was calculated as the number of grey hamsters captured divided by the number of active trap-days × 100.

In Nagorno-Karabakh, the long-term dataset for 1999–2023 comprised **36,617 active trap-days and 1,693 captured grey hamsters**, corresponding to an overall relative abundance of **4.62 individuals per 100 active trap-days**.

Annual relative abundance varied substantially during the monitoring period. The highest value was recorded in 1999, at **6.22 individuals per 100 active trap-days**, followed by **5.88** in 2000 and **5.39** in 2001. During subsequent years, relative abundance fluctuated but generally remained below the levels recorded at the beginning of the study. From 2017 to 2023, annual values remained below 4.0 individuals per 100 active trap-days, ranging from **3.52 in 2019 to 3.97 in 2023**.

These long-term fluctuations are consistent with pronounced temporal variation previously documented for grey hamster populations in the Martakert and Varnkatagh regions of Nagorno-Karabakh (Hayrapetyan et al., 2025). However, the present Martuni dataset is analysed independently and should not

be numerically combined with the Martakert–Varnkatagh dataset.

The temporal patterns of grey hamster abundance in the studied landscapes are shown in Figures 2 and 3.

Distribution across landscape zones

The distribution of *N. migratorius* captures and effective trapping effort among the studied landscape zones and localities is presented in Table 2.

In the lowland zone, **906 grey hamsters were captured during 18,799 active trap-days**, corresponding to a relative abundance of **4.82 individuals per 100 active trap-days**. In the foothill zone, **787 grey hamsters were captured during 17,818 active trap-days**, corresponding to **4.42 individuals per 100 active trap-days**.

Among the lowland localities, the highest relative abundance was recorded in Kakavadzor (**5.53 individuals per 100 active trap-days**), followed by Martuni (**4.58**) and Kajavan (**4.39**).

Variation among the three foothill localities was smaller. Relative abundance was **4.57** in Berdashen, **4.36** in Ashan, and **4.29** in Gishi.

During the 2024–2025 sampling period in the Republic of Armenia, **37 grey hamsters were captured during 1,355 active trap-days**, resulting in an overall relative abundance of **2.73 individuals per 100 active trap-days**. Relative abundance was **2.61** in Artashat and **2.82** in Armavir.

Thus, after standardization according to effective trapping effort, relative abundance was **4.82** in the lowland zone, **4.42** in the foothill zone, and **2.73 individuals per 100 active trap-days** in the combined 2024–2025 sample from the Republic of Armenia.

Because the Armenian observations cover only 2024–2025, whereas the Nagorno-Karabakh data represent long-term monitoring, these values describe relative abundance during different sampling periods and are not treated as directly equivalent long-term population trends.

Table 2. Distribution of grey hamsters across landscape zones

Landscape zone	Number of campaigns	Surveyed area (m²)	Total traps	Number of traps functioned	Non-functional traps	Animals captured	*Nothocricetulus migratorius*	Relative abundance per 100 active trap-days
Lowland zone	**265**	**8,243.64**	**26,500**	**18,799**	**7,701**	**6,633**	**906**	**4.82**
Kakavadzor (265–300 m a.s.l.)	84	1,753.64	8,400	6,025	2,375	2,133	333	**5.53**
Kajavan (400–450 m a.s.l.)	87	1,478.34	8,700	6,286	2,414	2,272	276	**4.39**
Martuni (approximately 400 m a.s.l.)	94	5,011.66	9,400	6,488	2,912	2,228	297	**4.58**
Foothill zone	**257**	**8,694.67**	**25,700**	**17,818**	**7,882**	**6,671**	**787**	**4.42**
Berdashen (750–800 m a.s.l.)	93	4,579.11	9,300	6,495	2,805	2,491	297	**4.57**
Gishi (650–700 m a.s.l.)	81	2,224.46	8,100	5,637	2,463	2,073	242	**4.29**
Ashan (700–750 m a.s.l.)	83	1,891.10	8,300	5,686	2,614	2,107	248	**4.36**
Republic of Armenia	**18**	**4,161.30**	**1,800**	**1,355**	**445**	**565**	**37**	**2.73**
Artashat (900–1,050 m a.s.l.)	8	1,264.00	800	575	225	215	15	**2.61**
Armavir (890–950 m a.s.l.)	10	2,897.30	1,000	780	220	350	22	**2.82**
Total	**540**	**21,099.61**	**54,000**	**37,972**	**16,028**	**13,869**	**1,730**	**4.56**

Relative abundance = number of Nothocricetulus migratorius *captured / number of functioning (active) traps × 100.*

Morphometric characteristics

Morphometric characteristics of male and female *N. migratorius* from the lowland and foothill zones of Nagorno-Karabakh and from the Republic of Armenia are summarized in Table 3. Sample sizes differed among traits because cranial measurements were available for fewer individuals than external

body measurements.

Mean body length (BL) was greater in males than in females within each geographic group. In the lowland zone, mean BL was **116.2 mm in males and 114.6 mm in females**. In the foothill zone, the corresponding values were **120.0 and 116.4 mm**, whereas in the Armenian sample they were **123.0 and 122.0 mm**, respectively.

However, geographic variation was not uniform across all traits. Although mean BL was greater in foothill than in lowland animals, mean tail length (TL) was greater in the lowland sample: **30.4 mm in males and 29.2 mm in females**, compared with **29.6 and 27.4 mm**, respectively, in the foothill sample.

A similar pattern was observed for hind-foot length (HFL). Mean HFL was **21.0 mm in lowland males and 19.9 mm in lowland females**, compared with **18.7 and 17.4 mm**, respectively, in foothill animals.

Mean ear length (EL) showed a different pattern. In males, mean values were similar between the lowland (**31.7 mm**) and foothill (**31.4 mm**) groups, whereas in females the foothill mean (**29.7 mm**) was higher than that of the lowland group (**28.7 mm**).

Cranial measurements also varied among geographic groups. Mean skull length (SL) was **24.0 mm in lowland males and 22.1 mm in lowland females**, **24.3 and 22.9 mm** in foothill males and females, and **30.4 and 30.0 mm** in the Armenian sample.

Mean zygomatic width (ZW) was greater in the lowland sample (**19.7 mm in males and 18.8 mm in females**) than in the foothill sample (**16.4 and 15.8 mm**, respectively). Mean interorbital width (IOW) was 14.4 and 12.8 mm in lowland males and females and 14.0 and 9.6 mm in foothill males and females, respectively.

For nasal length (NL), mean values were **6.0 and 5.8 mm** in lowland males and females, **5.8 and 5.6 mm** in foothill animals, and **6.3 mm in both sexes** in the Armenian sample. Mean nasal width (NW) was **6.1 and 5.9 mm** in the lowland group, **5.9 and 5.8 mm** in the foothill group, and **6.5 and 6.4 mm** in the Armenian group.

Mean body mass was **41.6 g in lowland males and 39.3 g in lowland females**, **41.2 and 38.3 g** in foothill males and females, and **48.9 and 48.8 g** in the Armenian sample.

Overall, the descriptive data demonstrate that geographic variation was **trait-specific rather than uniform**. The Armenian sample showed higher mean values for several traits, particularly body length, skull length, nasal dimensions, and body mass, whereas comparisons between the lowland and foothill populations differed according to the morphometric variable examined.

Table 3. Morphometric characteristics of the grey hamsterTable 3. Morphometric characteristics of the grey hamster

Trait	Sex	Lowland n	Min–max	M	m	SD	Foothill n	Min–max	M	m	SD	Armenia n	Min–max	M	m	SD
BL (mm)		109	100–125	116.2	0.75	7.86	123	96–127	120.0	0.62	6.91	17	116–127	123.0	0.82	3.39
		114	98–123	114.6	0.74	9.78	113	93–122	116.4	0.59	6.23	20	119–125	122.0	0.36	1.59
TL (mm)		109	28–34	30.4	0.10	1.06	123	27–30	29.6	0.07	0.76	17	26–38	33.0	1.00	4.14
		114	26–30	29.2	0.14	1.47	113	25–28	27.4	0.10	1.02	20	23–37	32.0	0.90	4.03
HFL (mm)		109	18–22	21.0	0.14	1.43	123	15–20	18.7	0.15	1.63	17	19–26	23.0	0.55	2.28
		114	16–21	19.9	0.16	1.69	113	14–19	17.4	0.16	1.66	20	20–25	22.5	0.32	1.43
EL (mm)		109	30–32	31.7	0.07	0.73	123	28–33	31.4	0.16	1.75	17	28–38	32.9	0.75	3.10
		114	27–29	28.7	0.07	0.72	113	26–31	29.7	0.17	1.78	20	29–36	32.1	0.44	1.98
SL (mm)		39	23–25	24.0	0.16	1.01	37	21–26	24.3	0.31	1.87	17	26–34	30.4	0.61	2.51
		43	21–23	22.1	0.15	1.00	37	21–24	22.9	0.19	1.13	20	27–32	30.0	0.39	1.74
ZW (mm)		109	17–21	19.7	0.16	1.65	123	15–17	16.4	0.06	0.71	17	16–22	19.8	0.42	1.73
		114	16–20	18.8	0.15	1.63	113	15–16	15.8	0.04	0.40	20	17–21	19.6	0.28	1.25
IOW (mm)		109	11–16	14.4	0.19	2.04	123	10–15	14.0	0.14	1.54	17	14–20	17.5	0.39	1.60
		114	10–15	12.8	0.15	1.69	113	0.9–14	9.6	0.56	5.95	20	14–20	17.6	0.30	1.35
NL (mm)		39	5.8–6.2	6.0	0.03	0.20	37	5.5–5.9	5.8	0.03	0.19	17	6.1–6.6	6.3	0.04	0.16
		43	5.6–6.0	5.8	0.03	0.19	37	5.3–5.8	5.6	0.04	0.24	20	6.1–6.5	6.3	0.02	0.11
NW (mm)		39	5.9–6.3	6.1	0.03	0.20	37	5.7–6.1	5.9	0.03	0.20	17	6.2–6.8	6.5	0.05	0.22
		43	5.7–6.1	5.9	0.03	0.19	37	5.6–6.0	5.8	0.03	0.20	20	6.2–6.7	6.4	0.03	0.14
Body mass (g)		109	27–53	41.6	0.96	10.00	123	25–50	41.2	0.79	8.79	17	28–55	48.9	1.99	8.20
		114	26–49	39.3	0.83	8.91	113	25–46	38.3	0.73	7.78	20	26–58	48.8	1.75	7.81

Abbreviations: BL, body length; TL, tail length; HFL, hind-foot length; EL, ear length; SL, skull length; ZW, zygomatic width; IOW, interorbital width; NL, nasal length; NW, nasal width; M, arithmetic mean; m, standard error of the mean; SD, standard deviation.

Sex structure

The sex structure of the sampled grey hamster populations varied among the studied localities (Figure 4). The figure presents the observed numbers of males and females and allows comparison of sex composition among the Nagorno-Karabakh and Armenian sampling sites.

Because locality-specific numerical counts underlying Figure 4 are not presented in Tables 1–3, no additional numerical estimates or inferential statistical tests are reported here.

Demographic structure

The demographic structure of the sampled grey hamster populations, based on the juvenile (Juv), subadult (Sad), and adult (Ad) age categories defined in the Materials and Methods, is presented in Figure 5.

The observed distribution indicates spatial variation in age-class composition among the studied localities. Because the locality-specific numerical age-class counts underlying Figure 5 are not included in Tables 1–3, exact percentages, pairwise mean differences, and inferential statistical significance are not reported here.

Discussion

The present study provides long-term information on the relative abundance of the grey hamster, *Nothocricetulus migratorius*, in lowland and foothill landscapes of the Martuni region, together with morphometric and demographic observations and a shorter comparative dataset from the Republic of Armenia. The principal findings are: (1) substantial temporal variation in relative abundance during the 1999–2023 monitoring period in Nagorno-Karabakh; (2) moderately higher relative abundance in the lowland zone than in the foothill zone; (3) lower relative abundance in the 2024–2025 Armenian sample than in the long-term Nagorno-Karabakh samples; and (4) geographic and sex-related morphometric variation that differed among individual traits rather than following a single uniform pattern.

Long-term variation in relative abundance

Standardization of abundance according to effective trapping effort substantially changes the interpretation of the trapping data. Based on 37,972 active trap-days, the overall relative abundance was 4.56 grey hamsters per 100 active trap-days. Within the long-term Nagorno-Karabakh dataset, 1,693 grey hamsters were captured during 36,617 active trap-days, corresponding to an overall value of 4.62 individuals per 100 active trap-days.

The annual data indicate marked temporal variation. Relative abundance was highest at the beginning of the monitoring period, reaching 6.22 individuals per 100 active trap-days in 1999 and 5.88 in 2000. Although abundance fluctuated during subsequent years, values recorded from 2017 to 2023 were consistently below 4.0 individuals per 100 active trap-days. Thus, capture-based relative abundance values were descriptively lower during the later part of the monitoring period than during the initial years of the study.

Long-term fluctuations are characteristic of many small-mammal populations because population size may respond to interacting effects of food availability, vegetation structure, climatic variability, reproduction, predation, and habitat disturbance. In the grey hamster specifically, considerable geographic variation in population status has been reported across its broad Eurasian range (Gromov & Erbajeva, 1995; Kryštufek & Vohralík, 2009). Regional studies have also documented substantial differences in occurrence and population status among landscapes. For example, Nedyalkov (2016) reported a restricted contemporary distribution of the species in Bulgaria and discussed the potential importance of intensive agricultural practices and habitat alteration.

Long-term observations from the Martakert and Varnkatagh regions of Nagorno-Karabakh likewise demonstrated pronounced temporal changes in grey hamster abundance (Hayrapetyan et al., 2025). The present results from the Martuni region therefore support the broader conclusion that populations of the species may undergo considerable temporal variation within the South Caucasus. Nevertheless, the Martuni and Martakert–Varnkatagh datasets represent different study areas and should be interpreted as independent population series rather than pooled quantitatively.

The lower relative-abundance values observed during the later part of the present monitoring period should therefore be interpreted cautiously. The available trapping data demonstrate temporal variation in relative abundance, but they do not by themselves establish a statistically tested long-term trend or allow the relative contributions of climatic conditions, agricultural practices, habitat modification, food availability, predation, or other environmental factors to be separated. These factors remain plausible mechanisms that require direct testing with corresponding environmental covariates.

Differences between lowland and foothill populations

After correction for active trapping effort, relative abundance was 4.82 individuals per 100 active trap-days in the lowland zone and 4.42 in the foothill zone. The difference between the two landscape zones was therefore smaller than suggested by calculations based on total trap placements.

Within the lowland zone, Kakavadzor had the highest relative abundance (5.53 individuals per 100 active trap-days), followed by Martuni (4.58) and Kajavan (4.39). The foothill localities were more similar to one another, with values of 4.57 in Berdashen, 4.36 in Ashan, and 4.29 in Gishi. These locality-level differences indicate that the distribution of the grey hamster cannot be explained by the broad lowland–foothill classification alone.

Such spatial heterogeneity is compatible with the known ecological flexibility of the grey hamster. The species occupies a broad range of open habitats, including steppe, semi-desert, agricultural, and anthropogenic environments, and occurs across a wide elevational range (Gromov & Erbajeva, 1995; Kryštufek & Vohralík, 2009). Its broad ecological distribution suggests that local habitat conditions may be at least as important as elevation itself in determining abundance.

Agricultural landscapes may have contrasting effects on grey hamster populations. Crops and associated vegetation can provide food resources, whereas intensive cultivation, soil disturbance, vegetation removal, and rodent-control practices may reduce habitat suitability or survival. Regional variation in these pressures has previously been considered relevant to the distribution and persistence of grey hamster populations (Nedyalkov, 2016; Hayrapetyan et al., 2025). However, because agricultural intensity and other habitat variables were not quantified as predictors in the present analysis, our results should be interpreted as demonstrating spatial differences in relative abundance rather than establishing their environmental causes.

Comparison with the Armenian sample

The combined relative abundance recorded in Artashat and Armavir during 2024–2025 was 2.73 individuals per 100 active trap-days, compared with 4.82 in the Martuni lowland zone and 4.42 in the foothill zone. At the locality level, relative abundance was 2.61 in Artashat and 2.82 in Armavir.

This difference is noteworthy but requires cautious interpretation. The Nagorno-Karabakh dataset covers 25 years of monitoring from 1999 to 2023, whereas sampling in Armenia was restricted to 2024–2025 and included only 18 surveys. Consequently, the Armenian value should not be interpreted as evidence that grey hamster populations are generally or historically less abundant in Armenia than in Nagorno-Karabakh. Rather, it represents the relative abundance recorded at the two Armenian localities during the specific sampling period.

Historical information indicates that the abundance and habitat associations of the grey hamster in Armenia may vary considerably among environments. Earlier regional literature reported low abundance in some natural habitats but substantially greater representation in human-modified environments (Sosnikhina, 1950; Yavruyan & Hayrapetyan, 2003). This further supports the need to distinguish geographic differences from differences caused by habitat type, sampling period, and local environmental conditions.

Continued standardized monitoring in Artashat and Armavir would therefore be necessary before temporal trends or persistent geographic differences could be evaluated reliably.

Morphometric variation

The morphometric data demonstrate clear geographic variation, but the direction of this variation differed among traits. This is important because the present data do not support a simple conclusion that animals from one landscape zone were uniformly larger than those from another.

Mean body length was greater in the foothill sample than in the lowland sample in both sexes: 120.0 versus 116.2 mm in males and 116.4 versus 114.6 mm in females. In contrast, mean tail length, hind-foot length, zygomatic width, and interorbital width were generally greater in lowland animals. Thus, the observed variation involved different components of body and cranial morphology rather than a consistent shift in overall body size.

The Armenian sample showed comparatively high mean values for several measurements. Mean body length reached 123.0 mm in males and 122.0 mm in females, while mean body mass was 48.9 and 48.8 g, respectively. Skull length and several other cranial measurements were also higher in the Armenian sample than in the two Nagorno-Karabakh groups.

Substantial morphological variation is consistent with previous knowledge of *N. migratorius*. The species has a broad geographic range and considerable geographic variation in external and cranial characteristics has been reported in regional and taxonomic accounts (Gromov & Erbajeva, 1995; Kryštufek & Vohralík, 2009). Morphometric variability has also been documented in Balkan material by Nedyalkov (2016).

The geographic differences observed in the present study may potentially reflect several non-exclusive factors, including environmental conditions, resource availability, demographic composition, age structure, or broader geographic differentiation. However, these mechanisms were not tested directly. Moreover, the Armenian morphometric sample was substantially smaller than the lowland and foothill samples, particularly for some traits. The comparatively high mean values observed in Armenia should therefore be regarded as descriptive evidence requiring confirmation with larger and temporally replicated samples.

Sex-related differences were also apparent for several traits. Males had greater mean body length than females in all three geographic groups, and male means were higher for a number of other measurements in the lowland and foothill samples. Nevertheless, sexual differences were not uniform across all traits. For example, mean nasal length was identical between males and females in the Armenian sample (6.3 mm), while mean interorbital width was slightly greater in Armenian females (17.6 mm) than in males (17.5 mm). Body mass was also nearly identical between Armenian males and females (48.9 versus 48.8 g).

Consequently, the present results do not support the earlier generalized statement that males exceed females in all morphometric characteristics. Instead, they indicate trait-specific sexual variation whose statistical significance should be evaluated using the corresponding individual-level measurements.

Sex and demographic structure

The observed sex and age composition varied among the studied localities (Figures 4 and 5). Such demographic heterogeneity is biologically plausible in small mammals because the proportions of males, females, juveniles, subadults, and adults can change with reproductive timing, recruitment, mortality, dispersal, and season of sampling.

However, interpretation of these patterns must remain proportional to the available data. Figures 4 and 5 illustrate variation among localities, but the locality-specific numerical counts used to construct these figures are not presented in Tables 1–3. Accordingly, the present analysis does not assign statistical significance to the apparent differences in sex ratio or age structure.

The demographic patterns nevertheless complement the morphometric results by demonstrating that the sampled populations were not identical in composition. Differences in age composition may also contribute to observed differences in body measurements among localities, because

morphometric traits can vary with age as well as sex. Future analyses based on individual-level data should therefore evaluate geographic area, sex, and age simultaneously rather than considering each factor independently.

Methodological considerations

A major methodological consideration emerging from the present reanalysis is the distinction between total trap placements and effective trapping effort. Of 54,000 trap placements, 16,028 were recorded as inactive, leaving 37,972 active trap-days. Using all trap placements as the denominator would systematically underestimate capture-based relative abundance.

Standardization by active trap-days produced an overall relative abundance of 4.56 individuals per 100 active trap-days and also changed locality-level estimates. This correction is particularly important when the proportion of inactive traps differs among sites or sampling periods.

At the same time, capture rate should be interpreted as an index of relative abundance rather than as an estimate of absolute population density. Differences in capture probability, animal movement, season, habitat structure, trap performance, and sampling design can influence trapping indices. The present study therefore uses the standardized term “individuals per 100 active trap-days” and avoids interpreting these values as absolute numbers of animals per unit area.

Several additional limitations should be considered. First, the duration of monitoring differed markedly between Nagorno-Karabakh and Armenia. Second, sample sizes for cranial measurements were smaller than those for external body measurements. Third, the available data do not permit direct testing of the environmental mechanisms potentially responsible for temporal and spatial differences in abundance. Finally, the descriptive demographic patterns require further analysis using the individual-level sex and age data underlying Figures 4 and 5.

Despite these limitations, the long duration of the Martuni monitoring series and the standardization of abundance according to effective trapping effort provide a useful baseline for evaluating temporal and geographic variation in *N. migratorius*. Together with previous observations from other parts of Nagorno-Karabakh (Hayrapetyan et al., 2025), the results demonstrate the value of continued standardized monitoring for understanding local population dynamics of this geographically widespread but regionally variable species.

The present study provides long-term data on the relative abundance, morphometric characteristics, and demographic structure of the grey hamster, *Nothocricetulus migratorius*, in the South Caucasus. Standardization of trapping data according to effective trapping effort was essential for obtaining internally consistent estimates of relative abundance. Across the complete dataset, 1,730 grey hamsters were captured during 37,972 active trap-days, corresponding to an overall relative abundance of **4.56 individuals per 100 active trap-days**.

Long-term monitoring in Nagorno-Karabakh from 1999 to 2023 revealed substantial interannual variation in relative abundance. Annual values were highest at the beginning of the monitoring period, reaching **6.22 individuals per 100 active trap-days in 1999**, whereas values recorded from 2017 to 2023 remained below 4.0 individuals per 100 active trap-days. Thus, capture-based relative abundance values were descriptively lower during the later part of the monitoring period than during the initial years. Because a formal temporal trend is not evaluated in the present analysis, these observations should not be interpreted as evidence of a statistically demonstrated long-term decline.

Spatial differences were also evident. Relative abundance was **4.82 individuals per 100 active trap-days in the lowland zone** and **4.42 in the foothill zone**. Among individual localities, values ranged from 4.29 to 5.53 individuals per 100 active trap-days. In the Republic of Armenia, the combined relative abundance recorded in Artashat and Armavir during 2024–2025 was **2.73 individuals per 100 active trap-days**. Because the Armenian dataset covers only two years and substantially fewer surveys, this difference should be regarded as a geographic and temporal comparison rather than evidence of a persistent long-term difference between regions.

Morphometric characteristics varied among geographic groups and between sexes, but the direction of variation differed among individual traits. Consequently, the data do not support a uniform pattern of larger body dimensions in any single landscape zone or a general conclusion that males exceed females in all morphometric characteristics. The comparatively high mean values observed for several traits in the Armenian sample are noteworthy but require confirmation using larger and temporally replicated samples.

The observed variation in sex and age composition further indicates demographic heterogeneity among the studied populations. However, more detailed evaluation of these patterns requires analysis of the individual-level data underlying the demographic distributions.

Overall, the results demonstrate substantial temporal, spatial, morphometric, and demographic variation in *N. migratorius* populations. The long-term dataset provides an important baseline for future monitoring in the South Caucasus. Continued standardized surveys using effective trapping effort, together with individual-level morphometric and demographic analyses and direct measurements of environmental variables, will be necessary to clarify the mechanisms underlying population change and geographic variation in this species.

Declarations

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Declaration of interest statement:

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this study.

Authors' Contributions

Vahram T. Hayrapetyan – conceptualization, methodology, project administration, field investigation, data collection, writing – original draft, and writing – review and editing.

Tigran A. Hayrapetyan – field investigation and sample collection.

Hasmik G. Khachatryan – literature review and data analysis.

Volodya S. Mirzoyan – field investigation and sample collection.

Karine V. Balayan – field investigation and sample collection.

Lusine G. Aydinyan – conceptualization, methodology, field investigation, data collection, writing – original draft, writing – review and editing, and correspondence.

Ethics approval and consent to participate

The long-term field research on small mammals was conducted in accordance with applicable national legislation and institutional ethical standards for research involving wild animals. The field programme in Nagorno-Karabakh, including the capture, handling, and collection of small mammals, was initiated under Permit No. 211, issued on 1 January 1998 by the Committee of Nature Protection of the Republic of Artsakh. The material from Nagorno-Karabakh used in the present study was obtained during the subsequent long-term monitoring programme conducted from 1999 to 2023.

Field research conducted in the Republic of Armenia was carried out within the Scientific Center of Zoology and Hydroecology of the National Academy of Sciences of the Republic of Armenia. The procedures involving animals were reviewed and approved in accordance with the applicable institutional and national ethical requirements. Ethical approval was confirmed by the National Center of Bioethics of the Republic of Armenia (Certificate dated 16 June 2025). According to this certification, the animal procedures were conducted in accordance with applicable international, European, and national ethical standards and guidelines for the use of animals in scientific research.

Throughout the study, appropriate measures were taken to minimize stress, suffering, and harm to the animals. No human participants were involved in this study; therefore, consent to participate was not applicable.

Consent for publication

Not applicable.

Data Availability Statement

The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request. Field data, morphometric measurements, and population monitoring records are stored in the archives of the Scientific Center of Zoology and Hydroecology of NAS RA and can be shared for research purposes under appropriate agreements.

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Figures

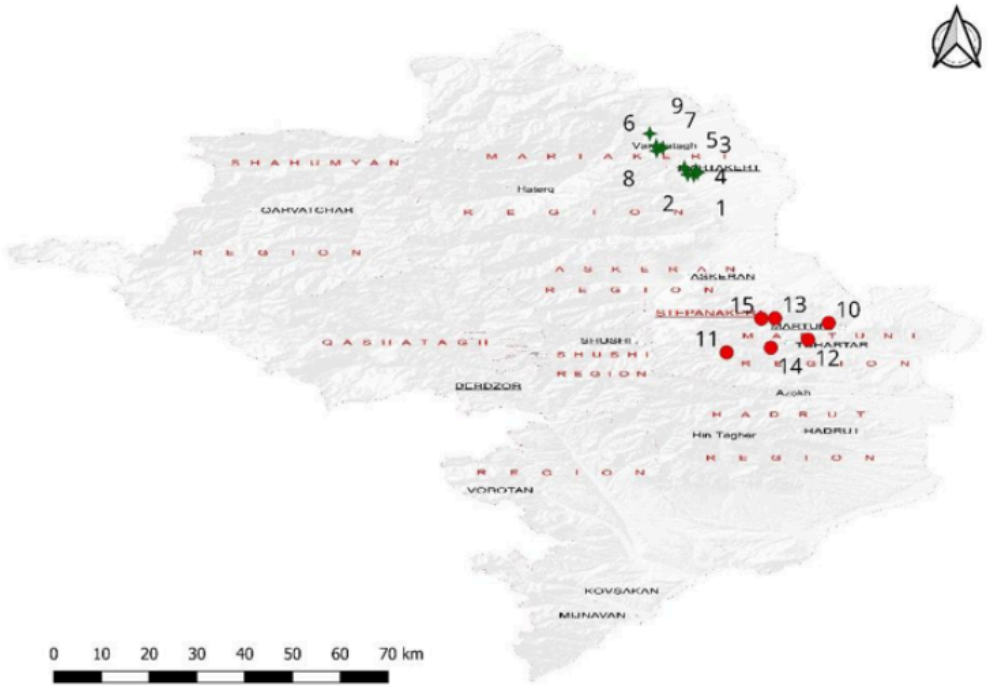


Figure 1

Sampling locations in the Martakert and Martuni regions of Nagorno-Karabakh. Sites 1–9 (Bagher, Kajavan, Arevdzor, Martakert, Dalakinaghbyur, Khachintap, Tigranintap, Mechaktap, and Ghushintumb), indicated in green, represent sampling locations in the Martakert region surveyed in 2025. Sites 10–15 (Kakavadzor, Kajavan, Martuni, Berdashen, Gishi, and Ashan), indicated in red, represent the Martuni-region localities included in the present long-term analysis. The Martuni dataset covers the period 1999–2023. Additional observations used for geographic comparison were conducted in Artashat and Armavir, Republic of Armenia, during 2024–2025.

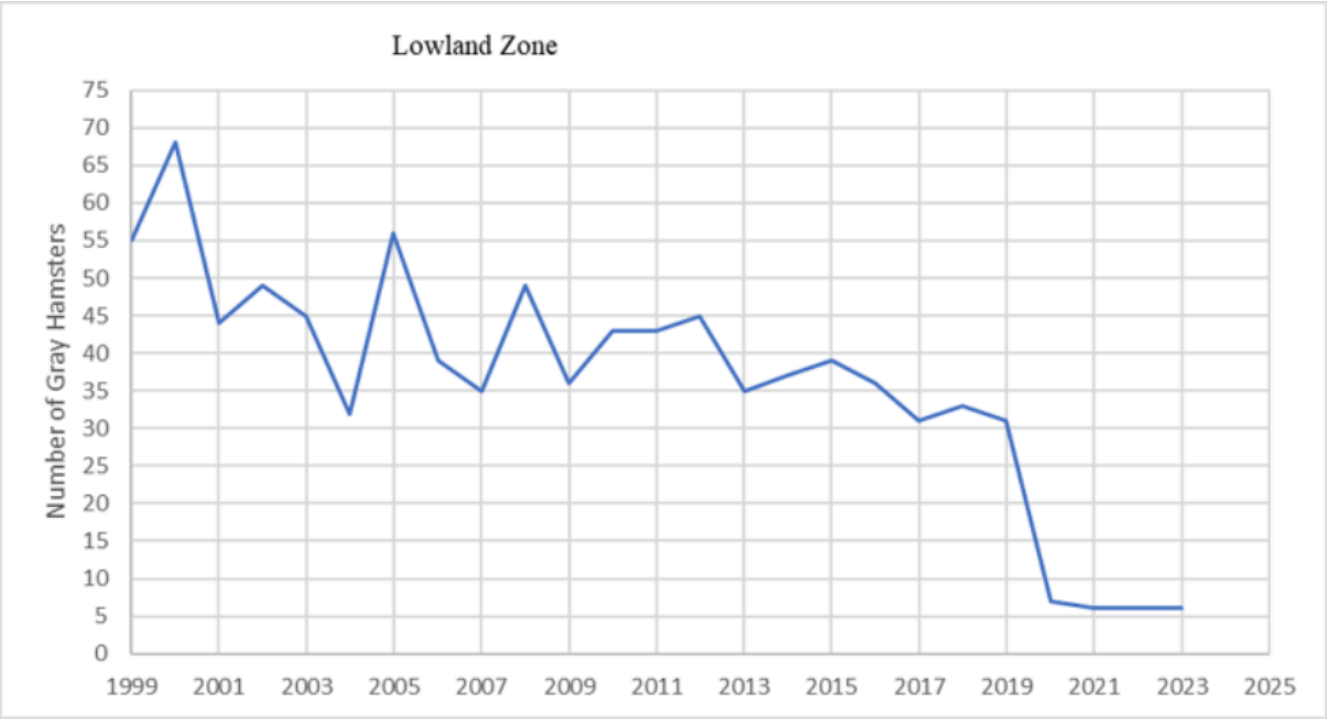


Figure 2

Population dynamics of grey hamsters (*Nothocricetulus migratorius*) in the lowland zone of Nagorno-Karabakh.

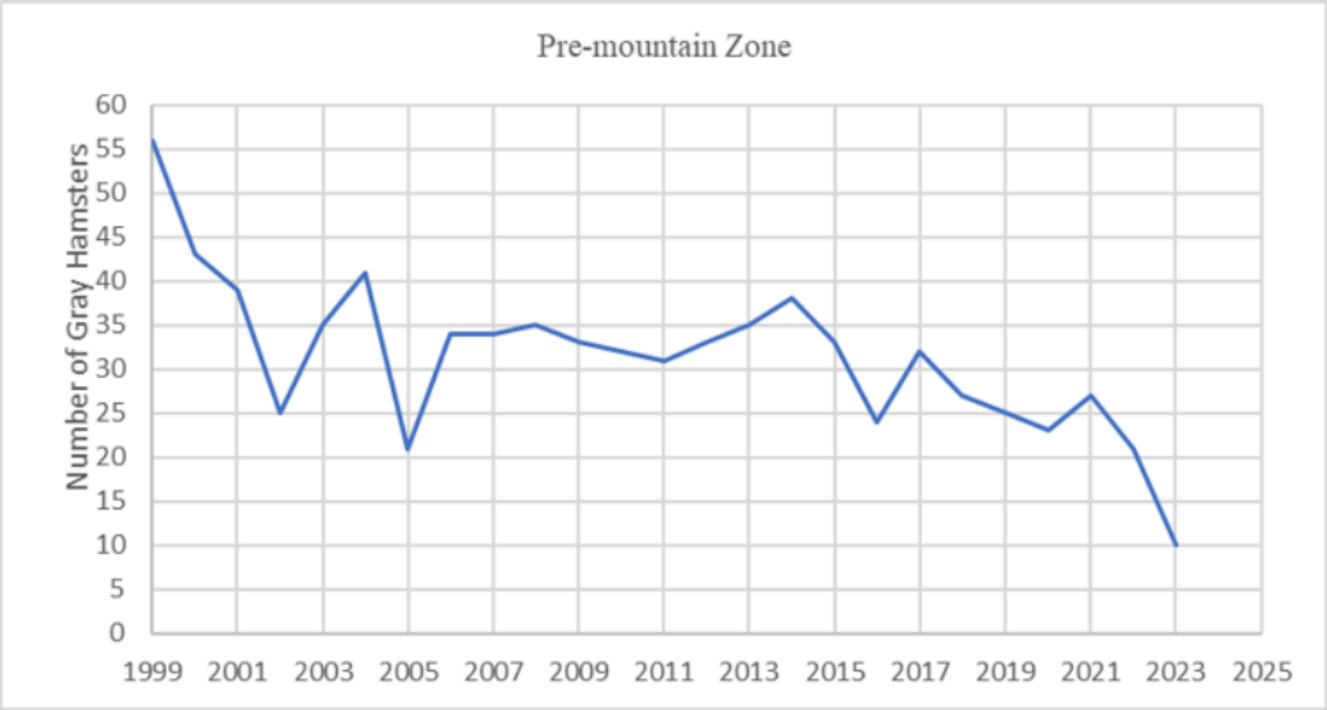


Figure 3

Population dynamics of grey hamsters (*Nothocricetulus migratorius*) in the foothill zone of Nagorno-Karabakh.

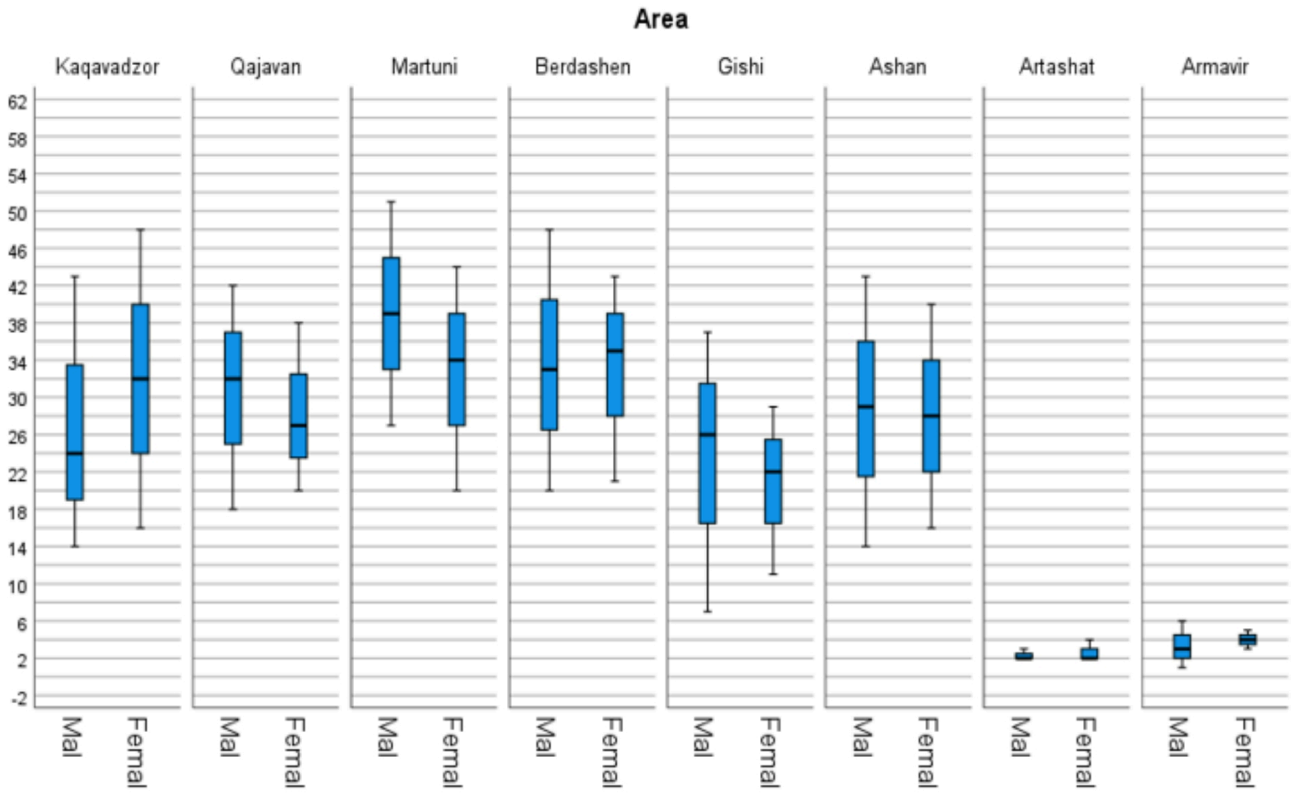


Figure 4

Sex structure of grey hamsters (*Nothocricetulus migratorius*) in the studied communities of Nagorno-Karabakh and the Republic of Armenia. The x-axis represents sex, and the y-axis represents the number of individuals.

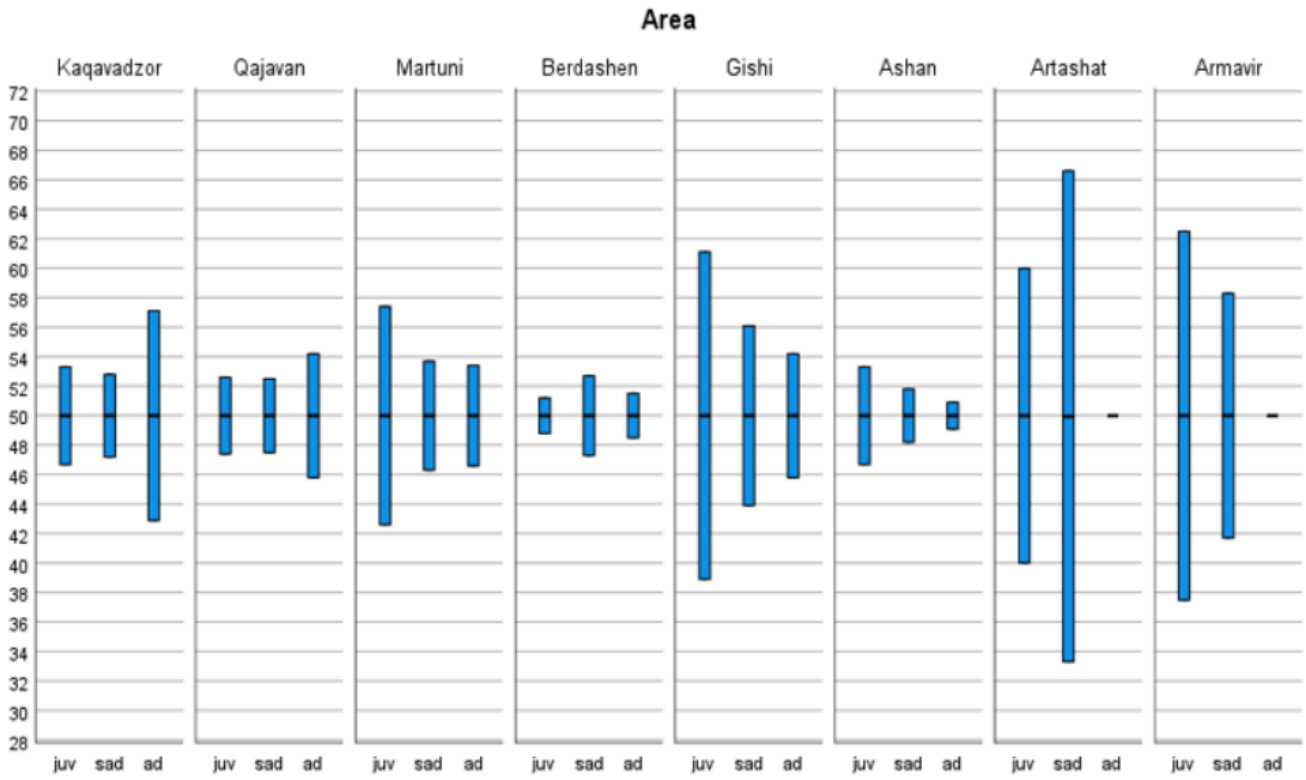


Figure 5

Demographic structure of grey hamsters (*Nothocricetulus migratorius*) in the studied areas of Nagorno-Karabakh and the Republic of Armenia. The figure shows the distribution of juvenile (Juv), subadult (Sad), and adult (Ad) individuals among the studied localities.