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Golden jackal (*Canis aureus*) in the Middle Volga region: genetic identification and range expansion

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ABSTRACT. The results of molecular genetic identification of two golden jackal (*Canis aureus*) individuals hunted in Penza Oblast, Russia, are presented. Identification was carried out using uniparental genetic markers (fragments of the cytochrome *b* gene and the mtDNA control region, together with the *ZfY* gene located on the Y chromosome) and a biparental genetic marker (the *ZfX* gene, localised on the X chromosome). The markers used confirmed that the individuals belong to the species *Canis aureus*. The data presented confirm the presence of jackals in the Middle Volga region outside the species' permanent range. The sequences obtained correspond to a haplotype of the Caucasian lineage that is widely represented among jackals dispersing across the European part of Russia. The chronology of the jackal's range expansion in the central and northern parts of the Russian Plain is analysed.

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KEY WORDS: Canidae, mtDNA, X and Y chromosome markers, Penza Oblast, Russia, range dynamics.

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Шакал (*Canis aureus*) в Среднем Поволжье: генетическая идентификация и расширение ареала

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РЕЗЮМЕ. Представлены результаты молекулярно-генетической идентификации двух особей шакала (*Canis aureus*), добытых в Пензенской области России. Идентификация проводилась с использованием однородительских (фрагменты гена цитохрома *b* и контрольного региона мтДНК, и гена *ZfY*, локализованного на Y-хромосоме) и двуродительских (ген *ZfX*, локализованный на X-хромосоме) генетических маркеров. Использованные маркеры подтвердили принадлежность особей к виду *Canis aureus*. Представленные данные подтверждают находки шакалов на Средней Волге за пределами зоны постоянного присутствия вида. Полученные последовательности соответствуют гаплотипу кавказской линии, широко представленному у шакалов, расселяющихся в европейской части России. Анализируется хронология расширения ареала шакала в центральной и северной части Русской равнины.

КЛЮЧЕВЫЕ СЛОВА: Canidae, мтДНК, маркеры X и Y хромосомы, Пензенская область, Россия, динамика ареала.

Introduction

The golden jackal (*Canis aureus* Linnaeus, 1758) is a species actively expanding its range across Northern Eurasia, including Russia (Stefanović *et al*., 2024; Politov *et al*., 2025). The expansion of *C. aureus* on the European continent is predicted to continue in the near future, driven by global climate change, anthropogenic landscape transformation and the low abundance of the apex carnivore — the wolf (Flores-Manzanero *et al*., 2026; Ranc *et al*., 2026). At present, according to the portal "Mammals of Russia" (https://rusmam.ru; Lissovsky *et al*., 2018), the jackal has been recorded in most regions (37 out of 55) of European Russia, from the steppes and semi-deserts of Ciscaucasia to the northern taiga and the White Sea coast.

In the Middle Volga region, located in the east of the Russian Plain north of the 52° N (Milkov, 1953), the jackal was first recorded in 2019 in Penza Oblast (Ermakov *et al*., 2022) and subsequently in 2024 in the Republic of Mordovia (Andreychev & Shkolov, 2024) and Samara Oblast (Kuzovenko *et al*., 2025). This species, new to the region, may have a negative impact on native ecosystems and game management, and may play a role in pathogen transmission (Gherman & Mihalca, 2017; Männil & Ranc, 2022).

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The northward dispersal of the jackal necessitates monitoring the species' distribution using genetic analysis, which enables accurate species identification and the detection of possible hybridisation. However, of the 134 jackal occurrence records on the "Mammals of Russia" portal made north of the species' permanent range (above 48° N), only four have been confirmed by molecular genetic methods: inter simple sequence repeat (ISSR) analysis in Moscow Oblast (Blokhina *et al*., 2018), sequencing of the mtDNA control region in Arkhangelsk Oblast (Rykov *et al*., 2022) and Pskov Oblast (Korablev *et al*., 2024), and sequencing of the mitochondrial cytochrome *b* gene together with a three-primer test for identification of the *ZfY* gene in Vladimir Oblast (Politov *et al*., 2025).

Here, we present data on the genetic identification of two jackal individuals from the Middle Volga region and analyse the chronology of range expansion in European Russia from 2018 to 2026.

Material and methods

Tissue samples were taken from a female and a male at two locations in the central and southern regions of Penza Oblast. The female jackal was hunted on 19 March 2022 in the vicinity of the village of Elshanka, Neverkinsky District (52.675° N, 46.624° E), while patrolling hunting grounds across an extensive area of meadow steppe at a distance of about 1 km from the settlement (Salagin, 2022). The male was hunted on 22 November 2025 in the vicinity of the village of Svishchyovka, Belinsky District (52.866° N, 43.693° E), together with two red foxes (*Vulpes vulpes*) during a dog-assisted hunt in the floodplain of the Bolshoy Chembar River, in the vicinity of a sheep farm where an attack by a jackal on domestic livestock had previously been recorded (Salagin, 2025). The species was preliminarily identified based on characteristic features of coloration and external morphology: reddish-grey fur with dark markings on the back and the tip of the tail, a whitish chin and throat, a short tail, and the fused digital pads of the middle toes. Both animals were young (yearlings), of normal body condition, with a dense and uniform coat. The age of the female was determined in the laboratory from the degree of wear of the upper incisors, and the age of the male from information provided by the hunters.

Molecular species identification was carried out using uniparental genetic markers (the control region (CR) and the cytochrome *b* (*cytb*) gene of mtDNA for the maternal lineage, and the *ZfY* gene on the Y chromosome for the paternal lineage) and a biparental genetic marker (the *ZfX* gene on the X chromosome). DNA was extracted by a standard procedure including treatment with sodium dodecyl sulfate and proteinase K and subsequent phenol–chloroform extraction (Sambrook *et al*., 1989). The following primer pairs were used: CR, L-Pro 5'–CGT CAG TCT CAC CAT CAA CCC CCA AAG C–3' (Douzery & Randi, 1997) and H576 5'–TTT GAC TGC ATT AGG GCC GCG ACG G–3' (Randi *et al*., 2000); *cytb*, GlCbstD 5'–AAT GAC ATG AAA AAT CAT CGT TGT–3' and GlCbendR 5'–CTT CAT TTT TGG TTT ACA AGA CCA–3' (Faerman *et al*., 2017); *ZfY*, Yint2-335 5'–GTC CAT TGG ATA ATT CTT TCC–3' (Shami, 2002) and YintR 5'–CAA GTT CTG CTT TGG TTC T–3' (Galov *et al*., 2014); and *ZfX*, U-ZF-2R 5'–GCC ACA AAT CAT GCA AGG–3' (Nakagome *et al*., 2008) and C-ZFX-F 5'–GTT CCC TTA AGG CAG GCA TA–3' (Tsubouchi *et al.*, 2012). The PCR protocol consisted of a 5 min denaturation step at 95°C, followed by 35 cycles of denaturation for 20 s at 95°C, primer annealing for 30 s at 56°C, and extension for 1 min at 72°C, with a final extension step at 72°C for 10 min. PCR products were purified by extraction from polyacrylamide gel. Sequencing was performed by the Evrogen company (Moscow, Russia) using the same set of primers as the PCRs. The sequences have been deposited in GenBank (PZ348788–89, CR, 559 bp; PZ348786–87, *cytb*, 930 bp; PZ348792, *ZfY*, 478 bp; PZ348790–91, *ZfX*, 501 bp).

Haplotype networks were constructed for the CR and *cytb* using the TCS algorithm in PopART 1.7 (Leigh & Bryant, 2015). For comparative analysis, CR (n = 127) and *cytb* (n = 51) sequences of jackals from the Palaearctic part of the range were retrieved from the NCBI GenBank database. After alignment, the length of the CR sequences was 229 bp, and that of the *cytb* sequences was 420 bp.

To analyse the range expansion of the jackal in the central and northern regions of European Russia, the map and data from the "Mammals of Russia" portal were used for a nine-year period, from 2018 to the first half of 2026. To visualise the range expansion, three periods were distinguished: 2018–2020, 2021–2023 and 2024–2026. The Kruskal–Wallis test, implemented in Statistica software (https://www.statsoft.com), was used to test for chronological differences in the latitudinal distribution of the jackal. Nine samples, corresponding to the years of observation, were formed based on 110 records of the species registered north of 48° N.

Results and discussion

Molecular genetic identification

The control region and cytochrome *b* gene sequences of mtDNA from the two jackals hunted in Penza Oblast corresponded to the most widespread *Canis aureus* haplotypes in the Palaearctic part of the range. The CR sequences we obtained are identical to haplotypes of jackals both from recently colonised regions — Arkhangelsk and Pskov oblasts of Russia, Finland, Spain, Lithuania, Belarus, Poland, and Ukraine (Kowalczyk *et al*., 2015; Paulauskas *et al*., 2018; Rykov *et al*., 2022; Korablev *et al*., 2024; Bogdanowicz *et al*., 2025) — and from areas within the permanent range — Bulgaria, Hungary, Serbia, Turkey, Azerbaijan, Georgia, Iran, and Israel (Randi *et al*., 2000; Rueness *et al*., 2011; Pilot *et al*., 2014; Shakarashvili *et al*., 2020; Barash *et al.*, 2023; Demirtaş, 2023; Ninausz *et al*.,

2023; Milanlou *et al*., 2024). Similar results were obtained for *cytb*. The haplotypes of the jackals from Penza Oblast are identical to those from Rostov and Vladimir oblasts of Russia, as well as from Hungary, Turkey, and Israel (Sosale *et al*., 2022; Demirtaş, 2023; Kazimirov *et al*., 2024; Koepfli *et al*., 2015; Politov *et al*., 2025).

The haplotype networks constructed for the two markers confirm a high degree of matrilineal genetic uniformity in the colonised part of the range — Eastern and Northern Europe — and diversity in its core — Western Asia and Southern Europe (Rutkowski *et al*., 2015; Milanlou *et al*., 2024; Bogdanowicz *et al*., 2025) (Fig. 1).

Genetic diagnosis of jackals from different regions of Russia has been carried out using different mtDNA markers: from Arkhangelsk and Pskov oblasts based on the CR (Rykov *et al*., 2022; Korablev *et al*., 2024), and from Vladimir and Rostov oblasts based on *cytb* (Kazimirov *et al*., 2024; Politov *et al*., 2025). The jackals from Penza Oblast were diagnosed by us using both mtDNA markers. Given the complete identity of the sequences obtained to those from other regions, and the inheritance of the mitochondrial genome as a single unit, we consider that all Russian specimens studied belong to a single mitochondrial haplotype of the Caucasian lineage (H1, Rutkowski *et al*., 2015).

The fragments of the final introns of the *ZfY* gene in the male and the *ZfX* gene in both individuals matched the previously studied sequences of *C. aureus* and differed from those typical of *C. lupus* and *C. familiaris* (Tsubouchi *et al*., 2012; Galov *et al*., 2014; Gürkan *et al*., 2023).

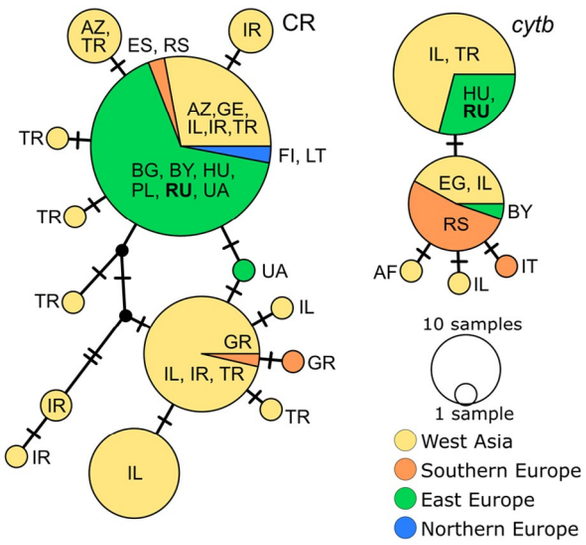

Fig. 1. Haplotype networks for *Canis aureus* based on an analysis of mitochondrial control region (CR, 229 bp) and cytochrome *b* gene (*cytb*, 420 bp) sequences. Sequences from the Penza Oblast and other regions of Russia are highlighted in bold. Countries are shown as two-letter codes (ISO codes).

Thus, all markers used, both mitochondrial DNA and sex chromosome markers, confirmed that the individuals from Penza Oblast belong to the species *C. aureus*. No evidence of first-generation hybridisation with the dog was detected, as there is no introgression for the maternal (mtDNA) and paternal (Y-chromosome) lineage markers, and no heterozygotes were found for the biallelic marker (X-chromosome). However, we do not exclude the possibility that genetically 'pure' jackals may result from the segregation of hybrid individuals, since the markers we used do not allow the detection of late-generation hybrids (F2, backcrosses).

Modern expansion of the range

The process of range expansion of the jackal within the territory of Russia in the late 20th and early 21st centuries has been examined in detail by Oparin *et al*. (2024) and Politov *et al*. (2025). Here, we analyse the current period of expansion, from 2018 to 2026. The choice of this time period is linked to the growing number of publications on jackal occurrences in territories new to the species, and to the creation in 2017 of the information system "Mammals of Russia" (https://rusmam.ru), which has made it possible, based on observations with precise dates and coordinates, to visualise three stages of expansion (Fig. 2).

In the west of the Russian Plain, the northward spread of the jackal occurred earlier than in the east. By the beginning of the period we analyse, jackal incursions had reached 52°–58° N and had been recorded in Belarus in 2011 (Kheidorova *et al*., 2018), in Estonia in 2013, in Latvia in 2014, and in Lithuania in 2015 (Paulauskas *et al*., 2018). At the same time, in the east of the plain, the northern limits of the species' permanent range ran approximately along 49° N. The jackal was numerous in the North Caucasus, particularly in Krasnodar Krai and the Republic of Dagestan, and was common in the Republic of Kalmykia and Rostov Oblast (Kudatkin *et al*., 2019; Stakheev *et al*., 2026). However, long-distance incursions by individual animals had been noted earlier: in 2007, an animal was hunted near Saint Petersburg, at 59° N (Abramov, 2007); in 2004, in the Saratov Trans-Volga region, at 50° N (Oparin *et al*., 2024); and in 2016, in the south of Moscow Oblast, at 54° N (Blokhina *et al*., 2018).

In 2018–2020, in the east of European Russia, the jackal was dispersing across the steppe and forest-steppe zones of the Volga region. Over these three years, 24 jackal records were registered north of the main range. In the Lower Volga region, *C. aureus* spread widely across the territory of Saratov Oblast, and in its southern districts became practically a common species (Oparin *et al*., 2024). In 2019, it was recorded for the first time in the Middle Volga region, in the south of Penza Oblast, having penetrated northwards to 52° N (Ermakov *et al*., 2022). In the west, in Kaliningrad Oblast, a jackal was hunted in 2020 on the Curonian Spit north of 55° N (Grishanova, 2020).

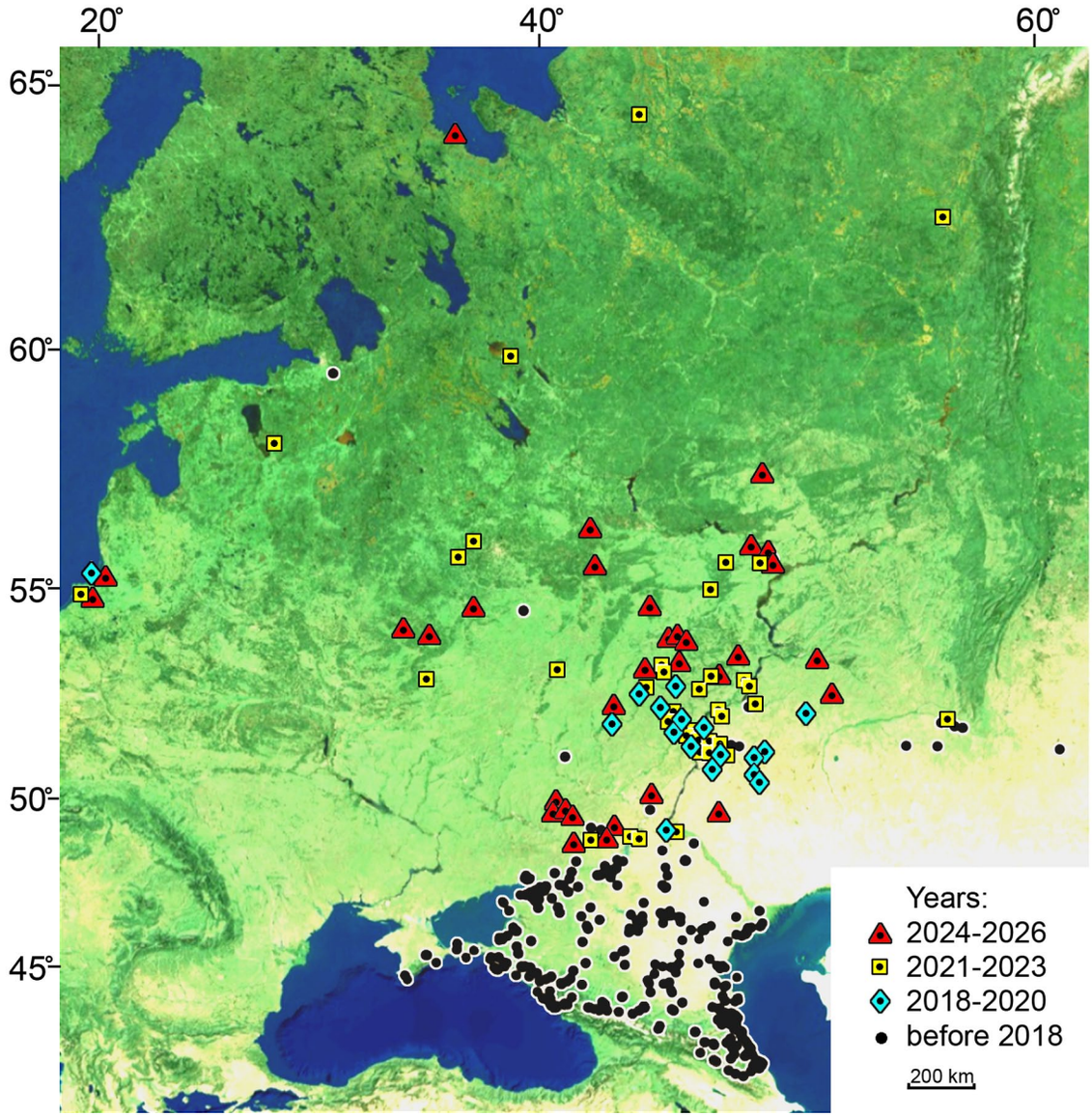

Fig. 2. Dynamics of the dispersal of the jackal (*Canis aureus*) across the territory of European Russia from 2018 to 2026, based on data from the information system "Mammals of Russia" (https://rusmam.ru).

In 2021–2023, the northward range expansion intensified considerably, both in the east and in the west of the territory under consideration. The number of records increased to 54. In Central Russia and the Volga region, the jackal advanced to 55° N and was recorded in Bryansk Oblast (Sitnikova, 2021), Moscow Oblast (Klimov, 2022), Lipetsk Oblast (Zemlyanuhin, 2023), and Chuvashia (Larionov, 2023). In the west, it was recorded in Pskov Oblast (Korablev *et al*., 2024) and Vologda Oblast (Stepanov, 2021), at 58° N and 60° N, respectively. During this same period, extreme incursions of the jackal into the north of Russia, into the northern and middle taiga forest zone, were recorded for the first time: in Arkhangelsk Oblast, at 64° N (Rykov *et al*., 2022), and in the Republic of Komi, at 63° N (Skumatov, 2022). In the neighbouring countries of Northern Europe, encounters with jackals were reported during this period in Norway and Finland, including north of the Arctic Circle (Sørensen & Lindsø, 2021; Kojola *et al*., 2024).

In the current period, 2024–2026, based on 32 records, the jackal is continuing to disperse across the central belt of Russia, including the sub-taiga forest zone. It has been recorded for the first time in Kaluga Oblast (Ermachenkov, 2026), Vladimir Oblast (Politov *et al*., 2025), and the Republic of Mordovia (Andreychev & Shkolov, 2024). In the Middle Volga region, it was registered in the Republic of Tatarstan, near Kazan (Monakhov, 2025), and subsequently crossed the Volga and penetrated into the Volga–Kama interfluve

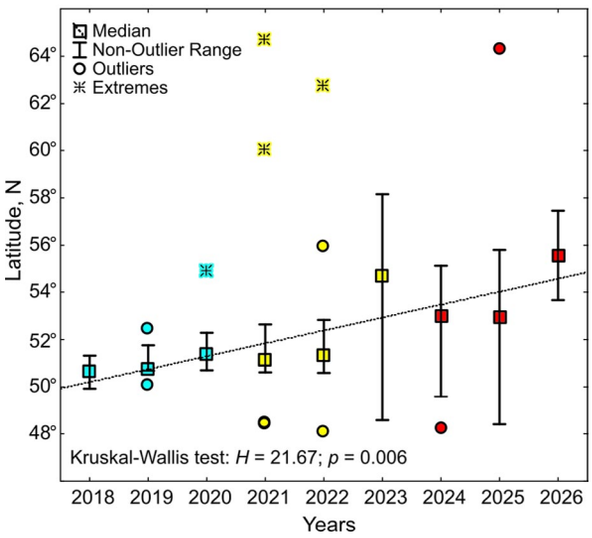

Fig. 3. Box plot of the geographic latitude values of jackal (*Canis aureus*) records by year of observation and the results of the Kruskal-Wallis test. Colors correspond to the chronological periods in Fig. 2.

in Kirov Oblast, reaching 57° N (Stepanov, 2026). On the left bank of the Volga, in the Trans-Volga region, where the northern limits of the range (50°–51° N) had remained practically unchanged since the beginning of the century, the species advanced northwards as far as the vicinity of Samara, reaching 53° N (Kuzovenko *et al*., 2025). In the north of Russia, in the Republic of Karelia, a jackal was detected on the White Sea coast, at 64° N (Tirronen, 2025).

The northward expansion of the jackal's range within the territory of European Russia during the period 2018–2026 is indirectly confirmed by non-parametric statistics. A comparison of the geographic latitude values of jackal records across the nine years of observations revealed significant differences between the groups according to the Kruskal–Wallis test (H = 21.67; p = 0.006) and a tendency for the median latitude values to increase (Fig. 3).

Conclusion

Thus, the genetic analysis of jackals from the Middle Volga region and comparison with previously published data suggest that across the territory of European Russia, from Ciscaucasia to the Subarctic, as well as in the majority of Eastern and Northern European countries, the dispersing jackals belong to a mitochondrial haplotype of the Caucasian lineage. The chronological analysis and visualization of the expansion periods point to the river valleys of the Don and the Volga as the most likely dispersal route of the jackal from the North Caucasian core of the range into the Volga region (Bogdanowicz *et al*., 2025; Politov *et al*., 2025).

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