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ORIGINAL ARTICLE

Species on the move: a genetic story of three golden jackals at the expansion front

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Abstract

One of the most fascinating mammalian range expansions in Europe involves an opportunistic mesocarnivore——the golden jackal (*Canis aureus*). However, key questions about the origins and dispersal strategies of pioneering individuals, likely the first to establish new populations, remain unanswered. We analyzed genetic data from three golden jackals found at the forefront of the expansion, reaching the Iberian Peninsula (Spain) and Fennoscandia (Finland and Norway, beyond the Arctic Circle). We genotyped two tissue samples and one fecal sample using 15 microsatellites and compared results with an extensive reference dataset. Additionally, we analyzed the mtDNA control region (HVR1) for two individuals. All individuals were males, identified as pure jackals and first-generation migrants. Our results suggested either western Pannonia (1650 km distance) or, less probably, the Adriatic region (1300 km) as the region of origin for the Spanish individual, also western Pannonia for the Finnish individual (2500 km), and the Baltics or the Caucasus for the Norwegian individual (1400 km to 3400 km). These sources represent abundant core populations or relatively recent and successfully colonized areas. Both the Spanish and Finnish individuals carried the prevalent H1 HVR1 haplotype in Europe, confirming matrilineal genetic uniformity on the continent. The recent expansion of *C. aureus* is fueled by several sources, showcasing the golden jackals' remarkable ability for long-distance dispersal as they extend their range to northernmost and westernmost Europe. Our findings highlight the dynamic nature of wildlife distribution, providing insights into species movement across vast distances amidst climatic, environmental, and anthropogenic pressures.

Keywords Expansion front · Europe · Long-distance movements · Mesocarnivore · Genetics · Pioneers

Introduction

The distribution of many terrestrial organisms is currently changing, primarily in response to climate change (e.g., Chen et al. 2011; see also Pacifici et al. 2020). For some species, particularly those with narrower niches and/or already living on the margins of their distribution, this will lead to challenges, range shifts, and contractions. Conversely, more adaptable species may find new opportunities to thrive. Almost 90% of mammalian species are expected to experience a reduction in range size, and a significant portion of these changes are presumably related to reduced dispersal abilities (Schloss et al. 2012) and climatic niche margins (Hampe and Petite 2005, Razgour et al. 2019; Pearman et al. 2024). Carnivores, however, are among the winners, as they are likely flexible to adapt to climate change and least constrained in terms of dispersal (Schloss et al. 2012). Dispersal is one of the key factors shaping ranges and community

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assemblages at local and large scales, and long-distance movements can determine the rate of population spread at the edge of a species' range (Trakhtenbrot et al. 2005).

One of the fastest and most fascinating mammalian range expansions and colonization of new areas in Europe is happening right before our eyes, and it is associated with an opportunistic mesocarnivore——the golden jackal (*Canis aureus*). In the 19th century, its European population was confined mainly to the coastal regions of the Mediterranean and Black Seas in southeastern Europe (Krofel et al. 2017; Spassov and Acosta-Pankov 2019). From the late 1960s and early 1970s, the species began to slowly expand its range, although its core distribution was still limited to southeastern Europe. The reasons were mainly changes in human attitudes toward jackals and implemented conservation measures (including the ban on poison baiting and usually temporary species protection), as well as favorable habitat changes (e.g., in Bulgaria, the creation of a widespread mosaic of shrubs that were impassable for livestock and served as jackals' shelters) (Spassov and Acosta-Pankov 2019).

A significant range expansion of the species was documented in the 1980s, first mainly along the eastern Adriatic coast (reviewed by Kryštufek et al. 1997) and then along the lowlands of southeastern and central Europe (Tóth et al. 2009). However, this expansion process has accelerated considerably over the past two decades (Spassov and Acosta-Pankov 2019), and in the north, golden jackals have crossed the Arctic Circle and reached the Barents Sea in northern Norway (Linnell et al. 2021; Sørensen and Lindsø 2021) and northern Finland (Kojola et al. 2024; Viranta et al. 2024). In the west, they have crossed the Pyrenees mountains and have recently been recorded in Spain (Sáenz de Buruaga et al. 2023). The current distribution of the golden jackal in Russia is also much larger than reported in the 20th century (Kudaktin et al. 2019; Rykov et al. 2022).

The drivers of this rapid expansion in golden jackals are still debated. Reasons are likely a combination of factors, including climate change (Fabbri et al. 2014; Cunze and Klimpe 2022), which is leading to an increase in habitat suitability (for review see Serva et al. 2023), deforestation and changes in land use (Šálek et al. 2014; Trouwborst et al. 2015), species plasticity [including high dietary flexibility, changes in the overall trophic niche, and flexibility of social behavior (Lanszki et al. 2022; Csányi et al. 2023)], adaptation to human-dominated environments (Fenton et al. 2021), and development of new dispersal strategies (Rutkowski et al. 2015; see also Lanszki et al. 2018). The historical decline of the grey wolf (*Canis lupus*) as an apex predator and competitor is also a factor to consider (Kryštufek et al. 1997; Krofel et al. 2017; Newsome et al. 2017; Karamanlidis et al. 2023; Serva et al. 2023; see also Wennink et al. 2019), although this biological constraint appears to have been mediated by the shielding effect of humans protecting golden jackals from grey wolves (N. Ranc and M. Krofel in litt.). Golden jackals in areas predicted to be suitable for wolves are also assumed to exploit different resources in more human-modified and open habitats (Serva et al. 2023). There are also indications that in some regions, both species may have altered their antagonistic relationship to become more tolerant of each other (Kudaktin et al. 2019; Guimarães et al. 2021; Theodoros Kominos, pers. comm.). Extrinsic factors, such as wartime conflicts (Tóth et al. 2009) and poor future prospects for space and food at the natal site (Kapota et al. 2016), as well as intrinsic factors, such as population waves toward the north outside the species' historical range, may have also promoted expansion (Rykov et al. 2022).

Documenting and monitoring the presence of golden jackal can be challenging due to the high possibility of confusing signs of occurrence with other, similar species, such as red fox (*Vulpes vulpes*), grey wolf, and raccoon-dog (*Nyctereutes procyonoides*). In such ambiguous events, genetic information can help to reliably verify whether the golden jackal has been roaming in an area. DNA-based assessments have already documented several source populations of the recent spatial expansion of golden jackals in Europe (e.g., Rutkowski et al. 2015; Stronen et al. 2021; Stefanović et al. 2024). Stefanović et al. (2024) also revealed admixture with dogs at the northern expansion front and in the recently expanded area across nearly the entire Eurasian range of the species. However, in expanding populations, the presence and reproduction of a species in new areas may be detected and reported with some delay, due to the low probability of observation resulting from low densities at the beginning of colonization, lack of knowledge about the species and confusion with other animals (McKelvey et al. 2008; see also Kowalczyk et al. 2020). Thus, it appears that information about truly pioneering individuals——the real explorers——at the species' leading range edges may be missing, so the origin of these particular animals is surrounded by uncertainty.

While the golden jackal's range expansion has been extensively documented, the genetic origins and dispersal strategies of pioneering individuals remain poorly understood. Despite the challenges, we managed to obtain biological samples from three jackals at the frontline of the expansion wave—beyond the Arctic Circle and on the Iberian Peninsula. We used 15 microsatellite markers to assess their population of origin, hypothesizing that they originated from geographically proximate areas with reproducing, demographically stable populations. Individuals at the vanguard of the expansion front are likely the best dispersers and are presumably the first to lay the foundation for new populations (Van Valen 1971). Obtaining genetic information on these founders will not only establish a necessary baseline but will also provide crucial knowledge for future monitoring of the species as it expands into new areas.

Methods

Samples

In our analyses, we utilized three biological samples of golden jackals originating from the edges of the species distribution range, two collected in Norway and Finland beyond the Arctic Circle and one from the Iberian Peninsula. The Norwegian jackal, documented through observation and remote camera traps, was identified from feces collected from snow on February 26, 2023, near Kåfjord at 69°27′53″ N, 20°31′52″ E in the county of Troms in northern Norway by a trained wildlife specialist. A pea-sized fragment of the scat was taken into a tube with silica to preserve both the sample and the DNA.

The Finnish individual was an adult male accidentally caught in a leg-hold fox trap and shot near the Lokka Reservoir in the municipality of Sodankylä at 67°25′27″ N, 27°70′87″ E in the county of Lapland on March 1, 2022. Its skin and skeleton (collection no. OV.35824) were deposited at the University of Oulu, Oulu, Finland (Viranta et al. 2024). A small fragment of the muscle tissue was used for DNA extraction.

The Spanish individual, the first in the Iberian Peninsula, was a male killed on the road in the municipality of Agurain/Salvatierra (42°51′09″ N, 2°3′22″ W) in the province of Álava on January 8, 2023. The specimen was deposited at the Centro de Recuperación de Fauna Silvestre de Mártioda in Álava (Sáenz de Buruaga et al. 2023). DNA was extracted from tissue taken from one of the ears.

Molecular analyses

Microsatellites

The DNA of golden jackals collected from Finland and Norway was extracted at NINAGEN, Centre for Biodiversity Genetics at the Norwegian Institute for Nature Research, Trondheim, for microsatellite analyses. Muscle tissue and scat sample were extracted using the Maxwell 16 Tissue DNA Purification Kit (Promega, Madison, WI, USA) following the manufacturer's protocol. The samples were genotyped at 15 autosomal microsatellite loci: CPH4, CPH5, CPH6, CPH8, CPH9, CPH12 (Fredholm and Wintero 1995), CPH22 (Dolf et al. 2000), FH2004, FH2088, FH2096, FH2137, FH2140 (Francisco et al. 1996), CXX.213, C09.250, C20.253 (Ostrander et al. 1993). An additional Y-chromosome marker (DBY7; Seddon 2005) was included for sexing purposes. The markers were amplified in two multiplex sets by polymerase chain reaction (PCR) using fluorescently-labeled forward primers and a multiplex PCR Kit (Qiagen, Hilden, Germany). PCR products were separated on an ABI 3500xl Genetic Analyzer (Applied Biosystems, Foster City, CA, USA) and allele sizes were assigned using GENEMAPPER v5.0 software (Applied Biosystems). The fecal sample was genotyped three times, and from these replicates, a consensus genotype was constructed by applying the following criteria: loci with a heterozygote result had to show this in two independent PCRs, while loci with a homozygote result had to show this in three independent PCRs.

The DNA from the Spanish jackal's was extracted using DNeasy Blood & Tissue Kit (Qiagen) according to the producer's protocol at the Museum and Institute of Zoology, Polish Academy of Sciences, Warszawa. The Spanish jackal was genotyped with the same microsatellites as those mentioned above. PCR amplifications were performed with two multiplexing sets (Multiplex PCR, Qiagen) using Veriti® Thermal Cycler (Applied Biosystems) under conditions following Rutkowski et al. (2015): denaturation at 95 °C for 15 min, annealing 40 cycles at 94 °C for 30 s, 57 °C for 90 s, 72 °C for 90 s and final elongation at 72 °C for 10 min (for loci: CPH4, CPH5, CPH8, CPH12, CPH6, CPH9, CPH22, FH2004, FH2088, FH2096, FH2137, FH2140) and denaturation at 95 °C for 3 min, annealing 35 cycles at 95 °C for 30 s, 57 °C for 45 s, 72 °C for 45 s and final elongation at 72 °C for 5 min (for loci: CXX.213, C09.250, C20.253). The results were analyzed using a CEQ 8000 sequencer (Beckman Coulter).

To calibrate scoring of allele sizes across labs, samples from three golden jackals, that had previously been genotyped in the DNA-lab at the Museum and Institute of Zoology PAS, were also genotyped at the DNA-lab at the Norwegian Institute for Nature Research.

Mitochondrial DNA

For two killed jackals, it was possible to obtain the hypervariable domain of the mitochondrial DNA (mtDNA) control region (HVR1). In the case of the Finnish individual, DNA was extracted at the University of Oulu from muscle tissue using the E.Z.N.A. ®Tissue DNA kit (Omega Biotek) following the manufacturer's protocol. Following Rutkowski et al. (2015), amplification of HVR1 was performed using the primers WDLOOPL (5′-TCCCTG ACACCCCTACATTC-3′) and H576 (5′-CGTTGCGGT CATAGGTGAG-3′). The PCR reaction mixture contained 2 µl of DNA, 1 µl of each 10 µM primer, 20 µl of PCR Master Mix (EURx), and 16 µl of purified water. The PCR profile in the Piko Thermal Cycler was set at 94 °C for 2 min, followed by 40 cycles at 94 °C for 15 s, 55 °C for

20 s, and 72 °C for 60 s, with a final extension at 72 °C for 2 min. The PCR product was purified by the alkaline phosphatase-Exonuclease I method (ExoSAP) and sequenced using the BigDye Terminator v.3.1 ® Kit and run on an ABI3730 (Applied Biosystems) sequencer.

In the case of the Spanish sample, DNA was extracted at the Departamento de Zoología y Biología Celular Animal of the University of the Basque Country in Vitoria-Gasteiz using DNeasy Blood & Tissue kit (Qiagen) according to the manufacturer's protocol. Following Vilà et al. (1999), amplification of HVR1 was performed using the primers Thr-L 15926 (5′-CAATTCCCCGGT CTTGTAAACC-3′) and DL-H 16,340 (5′-CCTGAAGTA GGAACCAGATG-3′). Alkaline phosphatase and Exonuclease I were used to purify the amplified product (i.e., to eliminate primers and excess deoxynucleotides). Finally, sequencing was done at Macrogen, Inc.

Statistical analyses

To define the population of origin of the three jackals, we compared their genotypes with a reference dataset representing the entire range of the species in Europe, including recently established populations. This dataset consisted of 346 individuals from 11 populations, representing: Baltic countries ($n=46$), Central Europe ($n=14$), Adriatic region ($n=11$), Pannonia (West) ($n=123$), Pannonia (East) ($n=29$), Campia Romana (= Wallachian Plain) ($n=43$), Thrace ($n=34$), Peloponnese Peninsula ($n=11$), Samos Island ($n=10$), Black Sea region ($n=11$), and the Caucasus ($n=14$) (Rutkowski et al. 2015; and unpublished data; see Fig. 1).

In all statistical analyses we used R Statistical Software, version 4.3.3 (R Core Team 2021). We employed Monte-Carlo and K-fold cross-validation procedures using the 'assign.kfold' and 'assign.MC' functions from the 'assignPOP' package (Chen et al. 2018). We applied five algorithms, including unsupervised (LDA) and supervised

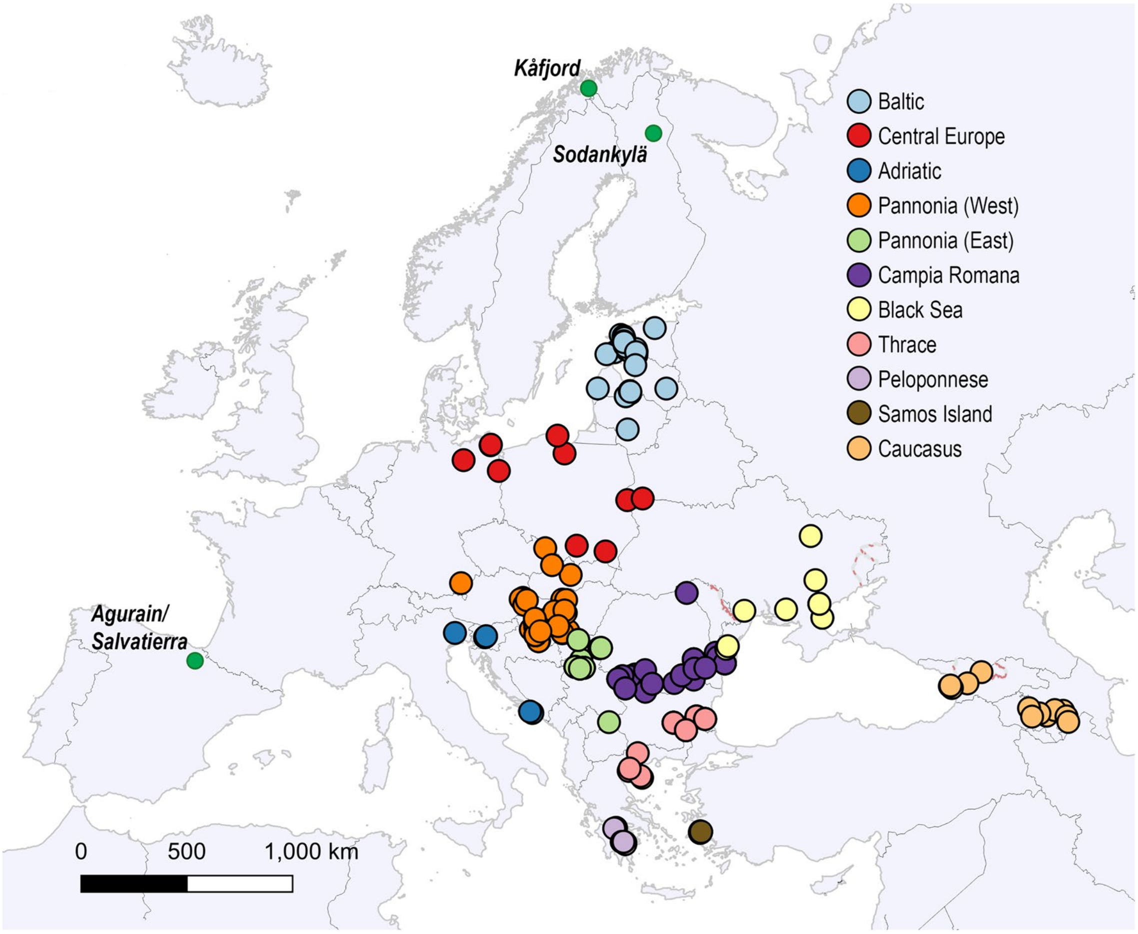

Fig. 1 Eleven regions grouping 346 golden jackal (*C. aureus*) samples used in comparison of the three genotypes originating from samples shown with their locality names, which were collected in Spain, Finland, and Norway (Rutkowski et al. 2015; and unpublished data; see "Materials and Methods")

learning (Naïve Bayes, SVM, decision tree, and random forest) to create predictive models with 'fst' and 'random' locus sampling methods and 30 iterations. For detailed checking, we focused on LDA, Naïve Bayes, and SVM, as the two other methods provided illogical results. In all these analyses, the proportion of individuals from populations was set to 0.7 and the proportion of loci was equal to 1. Each individual was assigned to the population of origin according to the most frequent population label selected.

Additionally, to trace back the origin of the three individuals, we employed GeneClass2 (Piry et al. 2004) with the frequency-based method (Paetkau et al. 1995) and the 'rubias' package in R (Moran and Anderson 2019). In 'rubias,' we applied the 'infer_mixture' function based on Bayesian inference for the conditional genetic stock identification (GSI) model (Moran and Anderson 2019). We also used the same option provided in 'rubias' to detect hybrids.

Knowing that jackals can travel long distances, we also checked whether the individuals were first-generation migrants. To do this, we used GeneClass2 (Piry et al. 2004) with the L = L_home/L_max option, i.e., the ratio of the likelihood (L) from the home population (L_home) over the highest likelihood value among all population samples (L_max) (Paetkau et al. 2004). We assumed that the individuals from Fennoscandia were from the Baltic population, while the individual from Spain came from the Central European or Adriatic population, i.e., in both cases our assumption was based on geographic proximity to the nearest breeding population.

To verify that the three jackals were not hybrids, we compared their genotypes against three clusters: (i) pure jackals ($n = 15$), (ii) mongrel dogs ($n = 9$), and (iii) jackal-dog(-wolf) hybrids ($n = 5$), using the Bayesian conditional GSI search in 'rubias'. The group of hybrid individuals consisted of samples numbered JHun9024, JUkr8600, JUkr8924, JHun9531, and JRom10658 in Table S6 in Stefanović et al. (2024), for which we performed microsatellite genotyping. This hybrid group contained individuals showing the jackal ancestry ranging from 0.483 (F1-generation) to 0.929 (distant but still some admixture) among all individuals analyzed by Stefanović et al. (2024). For each case, the three jackal samples were labeled as a 'mixture', and the training data sets were based on 15 microsatellite loci (listed above). Default parameters and the Markov Chain Monte Carlo (MCMC) method were implemented. The final label and status of the hybrid were determined based on the highest population assignment rate. To compare the mtDNA sequences obtained in this study, we searched for their homology within the *C. aureus* mitogenome, specifically using the GenBank accession no. NC_067757.1 (Sosale et al. 2023). We focused on the highly variable HVR1 segment at positions 15,521–15,770 (Rutkowski et al. 2015). This HVR1 sequence represented the H3 haplotype observed, among others, in the Caucasus and Asia Minor (Rutkowski et al. 2015; Sosale et al. 2023), and was used as a reference. By comparing our obtained sequences with this reference, we could assess their similarity and identify any variations (Table 1).

Results

The population of origin for the Finnish individual was consistently and with good support assigned to western Pannonia by all five methodological approaches used. For the Spanish individual, four methods pointed to western Pannonia, while the fifth method provided an equivocal result, indicating either western Pannonia or the Adriatic population. For the Norwegian sample, the indications were split between the Baltics (two methods) and the Caucasus (three methods; Table 2).

All individuals were identified as first-generation migrants. The 'migration' analysis performed in GeneClass2 suggested that both the Finnish and Spanish individuals came from western Pannonia, while the Norwegian individual came from the Caucasus (cf. Table 2).

A comparison with samples of dogs, hybrids and pure jackals using 'rubias' showed that all three individuals could be considered pure jackals. In each case, the probability of assignment to the reference group reached at least 0.988 (Table 3; see also Fig. 2).

Sequencing of the mtDNA revealed 483 bp and 440 bp fragments for the control region in the Finnish and Spanish jackals, respectively. These homologous fragments exhibited two nucleotide transitions, A15656G and A15752G, in relation to the reference (H3) sequence. Both fragments represented the H1 haplotype (see Table 1).

Table 1 Haplotype designations according to Rutkowski et al. (2015), considering variations in nucleotide positions in the HVR1 segment of the reference mitogenome, as observed in golden jackals from Europe and the Caucasus

Haplotype	Position			
	15,640	15,642	15,656	15,752
H1	T	C	G	G
H2	C	C	A	A
H3 (reference)	T	C	A	A
H4	T	C	A	G
H5	T	T	G	G

Table 2 Best assignments of the three golden jackals to the population of origin based on the three maximum likelihood models available in 'assignPOP', Bayesian conditional Genetic Stock Identification (GSI) in 'rubias', and Bayesian criteria in 'GeneClass2'

Individual	AssignPop			Rubias	GeneClass2
	Naïve Bayes	Support Vector Machine (SVM)	Linear Discriminant Analysis (LDA)	Bayesian conditional GSI	Bayesian criteria
Norwegian	Baltics (0.399)	Baltics (0.277)	Caucasus (0.366)	Caucasus (0.989)	Caucasus (83.2)
Finnish	Pannonia W (0.422)	Pannonia W (0.373)	Pannonia W (0.400)	Pannonia W (0.864)	Pannonia W (56.7)
Spanish	Pannonia W (0.396)	Pannonia W (0.400)	Pannonia W (0.420)	Pannonia W (0.837)	Adriatic/Pannonia W (49.4 / 44.6)

The values in parentheses represent the 'strength' of the assignment; and these values, as they represent different characteristics, should be read and compared vertically. In testing, 11 reference populations across the European continent (plus the Caucasus) were used

Table 3 Probability of assignment to dogs, hybrids, or pure jackals (reference) based on the bayesian conditional GSI search in 'rubias' with the entire set of microsatellites used

Individual	Group	Probability of assignment
Norwegian	Dog	0.000
	Hybrid	0.012
	Reference	0.988
Finnish	Dog	0.000
	Hybrid	0.000
	Reference	1.000
Spanish	Dog	0.000
	Hybrid	0.002
	Reference	0.998

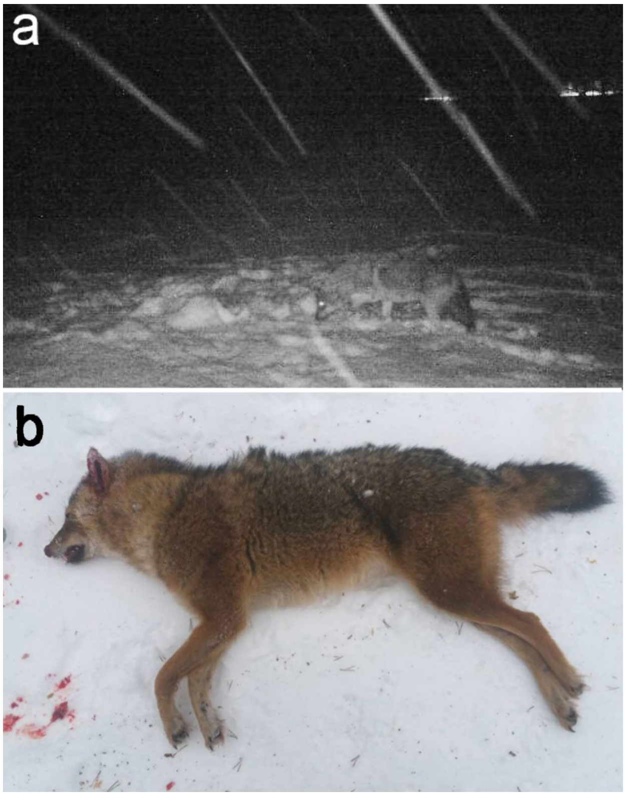

Fig. 2 Photos of the Norwegian (**a**) and Finnish (**b**) golden jackal (*C. aureus*) individuals. Credits to Maja Monsen and Seppo Mutilainen, respectively

Discussion

We employed genetic methods to trace back the origin of three golden jackals that embarked on impressive journeys, spanning vast distances across the continent up to the edges of Europe. All three individuals were identified as first-generation migrants. Based on their likely population of origin, the Norwegian individual seems to have covered a distance of at least 1400 km (the line from the Baltic countries circumventing the Baltic Sea) to 3400 km (from the Caucasus), while the Finnish individual appears to have traveled approximately 2500 km, and the Spanish individual covered from about 1300 (Adriatic region) to 1650 km (western Pannonia; Fig. 3). As a large part of the Baltic population originated from the Caucasus (Rutkowski et al. 2015; Stefanović et al. 2024), pinpointing the precise population origin for the Norwegian individual will require denser sampling in the Baltics and the Caucasus, likely combined with the use of higher resolution genomic data. In the case of the Spanish individual, the inferred origin encompassed two neighboring populations, including one (western Pannonia) that may already be saturated (see Csányi et al. 2023).

Surprisingly, the movements did not occur from the nearest breeding population, except possibly for the Norwegian individual (the assignment of the Spanish individual to the Adriatic population was ambiguous and lacked sufficient support). Recent confirmations of species reproduction came from Western and Central Europe, including south of the Po River in Italy (Travain et al. 2024), Germany (Böcker et al. 2023), Czech Republic (Jirků et al. 2018; Strnad et al. 2023), and Poland (Kowalczyk et al. 2020). On the other hand, these reproductive groups

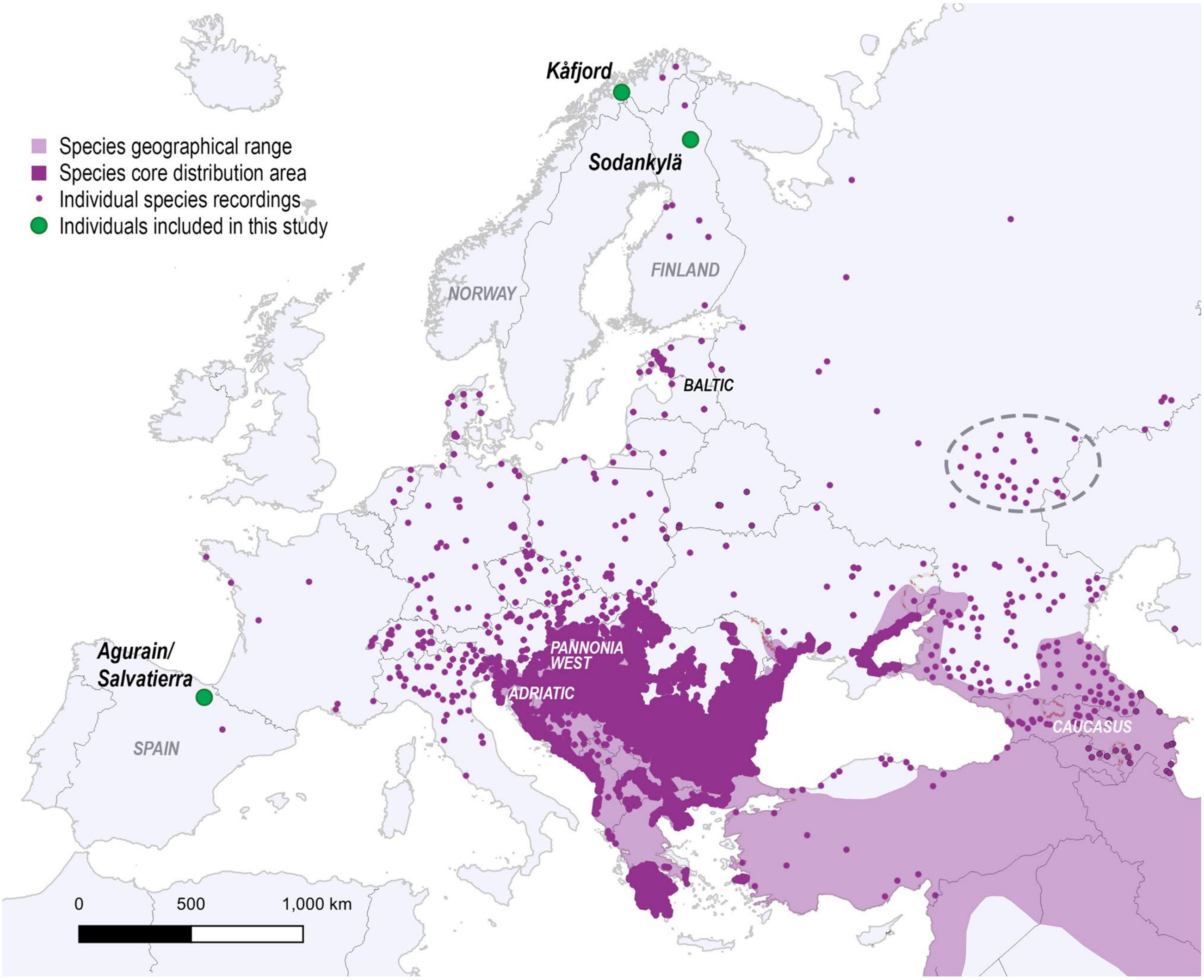

Fig. 3 The current distribution range of the golden jackal (*C. aureus*) in Europe, the Caucasus, and Asia Minor. Explanations to the map: the species geographical range——the range until 2018 with established, reproducing populations (Hoffmann et al. 2018); the species core distribution area——the strongholds (years 2012–2016) of the species distribution in southeastern Europe (Ranc et al. 2022). Individual species recordings were compiled from various sources, including MNHN & OFB (2003–2024), Rutkowski et al. (2015), Grichik et al. (2018), Hatlauf (2018), Lissovsky et al. (2018 and online updates), Spassov and Akosta-Pankov (2019), Shakarashvili et al. (2020), Tillmann (2020), Sørensen and Lindsø (2021), Frey et al. (2022), Lapini et al. (2022), Männil and Ranc (2022), Ranc et al. (2022), Voitko and Zagorodniuk (2022), Demirtaş (2023), Sáenz de Buruaga et al. (2023), Strnad et al. (2023), Kojola et al. (2024), Kowalczyk and Bogdanowicz (2024), Royo-Vicente and García (2024), and selected data (only for Turkey, Azerbaijan, and Kazakhstan) from https://www.gbif.org/species/5219219. The ellipse indicates the Saratov and Penza regions, representing a new nucleus of golden jackal presence in Russia

appear to be erratic and sensitive to habitat changes, typically consisting of a low number (usually a few) of individuals. In fact, dispersal was observed from abundant populations located in the species' core range or from relatively new but successfully colonized areas (Estonia in the Baltics), either as a result of escaping fierce competition and stress, such as high hunting pressure (probably in Pannonia) or as a result of seeking better chances for survival and fitness benefits (probably in the Baltics) (see Kapota et al. 2016).

However, it cannot be ruled out, that the northern expansion may somehow be related to other breeding populations that have not yet been detected or identified, for example, in the European part of Russia. Currently, there is a little support for this assumption——the haplotype (H1) of the mtDNA control region of the golden jackal recorded in the northern taiga subzone of European Russia was predominantly associated with populations from Europe and, to a lesser extent, the Caucasus (Rykov et al. 2022), although the easternmost occurrence of this haplotype has been documented in northeastern Iran (Milanlou et al. 2024). On the other hand, an important nucleus of golden jackal presence in Russia (most likely originating from the Caucasus, ca. 1100–1300 km away) has appeared in the Saratov and Penza regions, along the Volga River and its tributaries (see Fig. 3 and the Mammals of Russia portal at https://rusmam.ru/atlas/map—Lissovsky et al. 2018). This could potentially serve as a new source population for jackal colonization in western Russia, as well as Fennoscandia in the future.

The long-distance movements our results suggest (see also Fig. 3) indicate the golden jackal's notable capability to navigate diverse landscapes and environmental conditions, making this mesocarnivore a prime candidate for studying regional and continental range expansions. These dispersal movements are characterized by much longer step lengths compared to the home-ranging displacements, and they usually occur at night (Lanszki et al. 2018). Interestingly, the population of origin of both Finnish and Spanish jackals has been linked to the western part of Pannonia or nearby regions. The Pannonian population has already been suggested as an important source in the long-distance colonization of Central and Northern Europe (Rutkowski et al. 2015; Spassov and Acosta-Pankov 2019; Männil and Ranc 2022; Stefanović et al. 2024). However, the westward direction of this colonization process, through strongly modified environment with a dense road network (see Frangini et al. 2022), is a novel observation (cf. Kusza et al. 2019). On February 24, 2024, the second sighting of a golden jackal in Spain was recorded by a photo-trapping camera near Zaragoza in the community of Aragón at 41°39′22″ N, 0°52′64″ W (Royo-Vicente and García 2024). Additionally, in February 2023, a golden jackal was captured on camera in Plonéour-Lavern, Brittany, France at 47°5′13″ N, 4°16′57″ W (Moreau 2023), signifying its presence along the Atlantic coast (Fig. 3). Likely, new sightings and recordings on the Iberian Peninsula are to be expected in the near future.

For recent expansion, changing climate is likely one of the key factors. Golden jackals have recently been documented at higher elevations in the Italian Alps (http://gojage.blogspot.com/2019/09/jackals-in-alps-italy.html*)* and the Caucasus (Shakarashvili et al. 2020). Globally, the golden jackal's altitudinal range spans from sea level in the deserts of Saudi Arabia (Eid and Smithson 2024) to 4724–5365 m a.s.l. in the Trans-Himalayan Region (Khan et al. 2024) and may serve as further proof of climate influence and the species' high adaptability. Recent findings in the Trans-Himalayan Region raised the highest recorded altitude of golden jackals by approximately 2000 m.

Long-distance dispersal involves movement both beyond the geographic boundaries of the species and the genetic neighborhood of individuals (Jordano 2017). In theory, such movements should lead to a decrease in genetic diversity as distance from the source of expansion increases (Excoffier et al. 2009). However, the research conducted by Stefanović et al. (2024) revealed that there was no reduction in genetic diversity of golden jackals at the expansion front. This rather unexpected finding was attributed to multiple waves originating from distinct source populations, as well as the potential introgression of genetic variants from dogs. Remarkably, even the jackals found north of the Arctic Circle in Finland and Norway came from entirely different source populations: western Pannonia and either the Baltics or the Caucasus, respectively.

Stefanović et al. (2024) also observed signatures of dog admixture among golden jackals at the northern edge of their range and in recently expanded areas across Eurasia. However, whether an individual represents a hybrid should always be tested on a case-by-case basis, as in our study, where none of the examined genotypes exhibited signs of hybridization with dogs (see also Viranta et al. 2024). In terms of appearance and morphology, the two photographed individuals closely resembled pure jackals, as depicted in Fig. 2, although phenotypic traits can sometimes be misleading. For example, despite the suspicious phenotypic features found in the three suspected hybrid jackals in Hungary, none of them was detected as a genetic outlier in the study by Kusza et al. (2019). A genetic study conducted by Ninausz et al. (2023) highlighted that among various fur colors, ranging from white through agouti to black, only black and mottled individuals were identified as (recent) hybrids.

In the two individuals originating from western Pannonia and/or surrounding areas, we detected the H1 mtDNA control region haplotype, which is the most common in Europe, confirming a high degree of matrilineal genetic uniformity (e.g., Zachos et al. 2009; Fabbri et al. 2014; Rutkowski et al. 2015). Even among jackal-dog hybrids and animals resembling jackal hybrids from continental Europe, this haplotype is overwhelmingly dominant. In the Carpathian Basin, out of 31 individuals with fur color aberrations, 30 possessed the same H1 haplotype. The sole exception was one animal that showed possible dog maternity (Ninausz et al. 2023). These findings suggest that most hybridization events occur between female jackals and male dogs (see also Galov et al. 2015), and this sex-biased directionality in wild canids and dogs seems to be quite typical (Leonard et al. 2013). The absence of hybrid characteristics in all three jackals studied may imply that they were indeed pioneers, the first colonizers of uncharted territory, captured on the move, in the act of exploration.

All three golden jackals were males, prompting the question whether long-distance movement is male-biased, following a common trait observed in many social and solitary carnivores (e.g., Biek et al. 2006). From a genetic perspective, the similarity of spatial autocorrelation patterns in both sexes, as recorded by Stefanović et al. (2024), does not provide support for sex-biased dispersal. Additionally, observations and radiotracking data suggest that both males and females can disperse over larger distances (e.g., Lanszki et al. 2018; see also Rutkowski et al. 2015). An experimental study by Kapota et al. (2016) revealed differences in dispersal rates between age classes, with subadults emigrating more often than adults, but no differences were noted between the sexes.

The presence of golden jackals in the Far North in winter, exemplified by the Finnish and Norwegian individuals, suggests that the species is capable to surviving harsher conditions. This fact also indicates the existence of suitable habitats for jackals in northern Europe, at least seasonally. In Estonia, such habitats are found along heterogeneous coastal regions, where winters are milder and snow cover is more limited (Männil and Ranc 2022). However, evidence suggests that the species can also live in areas with seasonally thick snow cover, including in high mountains (e.g., Shakarashvili et al. 2020), relying, at least in part, on food left by humans (see also Krofel et al. 2023). The stomach of an individual from Finland contained, among other things, fish remains, which were probably leftovers discarded by local fishermen (Viranta et al. 2024). In contrast, the stomach of the Spanish individual revealed wild boar (*Sus scrofa*) hairs (Sáenz de Buruaga et al. 2023). According to a meta-analysis conducted by Lanszki et al. (2022), jackals in newly established territories showed a higher frequency of consuming small mammals and/or wild ungulates, primarily through scavenging, and a lower frequency of consuming plants and/or domestic animals (which were also mainly acquired through scavenging).

Understanding the enlargements and shifts in range and their impact on ecological communities is crucial for effective conservation and species management. Spotting a golden jackal in a new region or country typically triggers a debate about how to manage the newcomer. Despite the species spreading naturally across Europe and Asia (e.g., Rutkowski et al. 2015; Stronen et al. 2021; Khan et al. 2024; Stefanović et al. 2024), it is often perceived as an alien and even invasive species. Legislation and policy on naturally expanding species is quite clear (Trouwborst et al. 2015). The Habitats Directive designates the golden jackal as a protected species under Annex V. This means that, at the very least, European Union countries are obliged to maintain the favorable population status of the species. However, to mitigate conflicts, early detection of first arrivals, e.g., through DNA and visual identification, can facilitate scientifically-based dialogue between wildlife management authorities and the public, as well as for informed wildlife management decisions.

The rapid spread of golden jackals raises important inquiries for wildlife management agencies and legal frameworks (e.g., Trouwborst et al. 2015; Hatlauf et al. 2021). Golden jackals occupy a key niche in the ecosystem, and their territorial expansion could lead to significant alterations to predator-prey, scavenger-prey, and host-parasite relationships within the newly colonized regions (Gherman and Mihalca 2017). Given that jackals serve as hosts to a wide variety of canine and zoonotic parasites, it is important to recognize that they may play an important role in transmitting infections to both domestic animals and humans (reviewed by Veronesi et al. 2023). However, existing studies have not definitively provided conclusive evidence of adverse ecological consequences resulting from this rapid spread (but see Krofel et al. 2022). This complex scenario underscores the need for further investigation to fully understand the consequences of its presence.

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Data availability The HVR1 mtDNA sequences of the samples have been deposited in the NCBI GenBank public sequence repository and are available under the accession numbers PP551936 and PP551937. Microsatellite genotypes are partially available in Rutkowski et al. (2015), with the rest available upon reasonable request.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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