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RESEARCH ARTICLE

Genetic characterization of populations of the golden jackal and the red fox in Israel

Tali Magory Cohen · Roni King · Amit Dolev · Amitzur Boldo · Anat Lichter-Peled · Gila Kahila Bar-Gal

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Abstract The golden jackal and red fox are among the wildlife species protected by Israeli law as enforced by the Israel Nature and Parks Authority. In 1964, as a part of a management program to control rabies in Israel, a poison eradication campaign was launched to exterminate golden jackals, considered to be the main reservoir of the disease. The program resulted in the near-complete extermination of jackals in Israel, while foxes were only mildly affected. Jackals have since regained their original numbers and have recolonized southern Israel. We here examined the population structure of the golden jackal and red fox in Israel, 48 years after the poison eradication campaign. DNA from 88 golden jackals and 89 red foxes representing five different geographic regions was extracted and amplified at 13 microsatellite loci in order to characterize the populations on a genetic level. High genetic diversity was found among the jackal and fox populations. A possible migration route through the Jordan Rift Valley was suggested for both species by the genetic similarity of populations in northern and southern Israel. However, in both species, the animals from the center of Israel were distinctive from those north or south, indicating the relative isolation of central populations, likely due to fragmentation or a high abundance of food resources. Genetic profiles obtained for the golden jackal and the red fox in Israel may aid in their conservation management and in the study of zoonotic diseases.

Keywords Golden jackal · Red fox · Population genetics · Microsatellites

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T. Magory Cohen · A. Lichter-Peled · G. Kahila Bar-Gal (✉)
The Koret School of Veterinary Medicine, The Robert H. Smith Faculty of Agriculture, Food and Environment, The Hebrew University of Jerusalem, 76100 Rehovot, Israel
e-mail: kbgila@gmail.com

R. King · A. Boldo
Nature and Parks Authority, Jerusalem, Israel

A. Dolev
Israel Mammal Research Centre, The Society for the Protection of Nature in Israel, 66183 Tel-Aviv, Israel

Introduction

As a terrestrial crossroad between different biogeographic regions (Irano–Turanian, Mediterranean, and Saharo–Arabian), Israel has a diverse fauna and flora. During the last century, over 45 species of animals and 30 % of its flora have become extinct, mostly due to anthropogenic factors (Shalmon 1999; Dolev and Perevolotsky 2004; Shmida and Polak 2008). Dozens of animal species and more than 400 plant species are currently endangered (Dolev and Perevolotsky 2004; Shmida and Polak 2008). The decline of biodiversity in Israel is primarily the result of accelerated development, population growth, and the destruction of habitat, all contributing to the main problem challenging conservation efforts in Israel—habitat fragmentation (Gabbay 1997). Moreover, many populations of wild species in Israel reside outside of protected areas and are subject to disruption caused by roads, human settlements, and man-made barriers. Human–animal conflicts that arise due to the reduction in natural habitats such as road-kill, poisoning, and other factors pose additional threats to many species, including wild canids such as golden jackals (*Canis aureus*) and red foxes (*Vulpes vulpes*) (Yom-Tov and Mendelssohn 1988).

In the past, management of wild canids in Israel was conducted through the use of poison (Mendelssohn 1972). In 1964, a large-scale poison eradication program was launched in Israel by the Plant Protection Department of the Ministry of Agriculture to exterminate golden jackals that were considered the main reservoir of rabies. It resulted in the near-complete extermination of jackal populations in Israel, although red foxes were not greatly affected. A deep reduction in population size is generally referred to as a population bottleneck, which can result in very low levels of genetic variation (Nei et al. 1975; Chakraborty and Nei 1977; Nei 1977; Leberg 1992). In large populations, most allele frequencies are stable over long periods of time (England et al. 2003). Small, isolated, and fragmented populations lose genetic diversity over time through inbreeding and genetic drift (Ellstrand and Elam 1993; Lacy 1997; Frankham and Ralls 1998; Chevolot et al. 2008). Due to the drastic reduction in the jackal population size during the 1960s, they became vulnerable to extirpation. Enforcement of laws that protect wildlife together with conservation actions executed by the Israel Nature and Parks Authority (INPA) subsequently helped the jackal population increase to previous levels. Nonetheless, in agricultural areas, jackals and foxes are considered pests because they damage irrigation equipment and prey on livestock (Moran and Keidar 1993; Nemtzov and King 1998; Yakobson et al. 1998; Nemtzov and King 2002; Nemtzov 2002). This, along with limited habitat space in Israel, a consequence of growing human populations, has led to conflicts between humans and wild canids.

Today, the golden jackal and red fox are found in Israel in large numbers, yet remain protected by wildlife conservation laws. Their ability to adapt to anthropogenic changes has allowed them to disperse to southern Israel, although they did not previously reside in the desert environment (Nemtzov and King 2002). Dispersal acts as an important agent increasing genetic variability among wild animal populations (Frankham et al. 2002); we thus sought to determine dispersal patterns among jackals. Among canids, golden jackals and red foxes share many physiological and behavioral features as well as similar ecological niches and both thrive in proximity to humans (Mendelssohn and Yom-Tov 1999; Lanszki and Heltai 2002). Thus, we sought to compare the jackal population to population of the red fox, as a “control” species that, unlike the jackals, had not undergone a previous severe reduction in population size (Frankham 1995). Neither of these species had been studied extensively genetically in Israel. We wanted to determine whether geographic and topographic features, or the fragmentation of habitats by human settlements and transportation routes may have led to differentiation between populations by affecting connectivity between subpopulations of wild canids in Israel.

Materials and methods

Sample collection

Blood and tissue (ears of carcasses) samples of golden jackals and red foxes were collected in Israel between the years 2000 and 2011 by INPA rangers (Supplementary Table 1). In order to verify the taxonomic identity of the tissue samples prior to the study, a region of 210 bp of the mitochondrial gene MT-RNR1 (12S) was amplified (Roca et al. 2005) and directly sequenced using the ABI PRISM 3700 DNA Analyzer (Applied Biosystems, USA) at the Center for Genomic Technologies at the Hebrew University of Jerusalem.

The samples used for the study originated from different geographic regions across the country, including isolated areas. A total of 88 golden jackal and 89 red fox individual samples were collected and ascribed to one of five geographic regions in Israel, delineated based on climate and geographic terrain (Fig. 1) as follows: the Golan heights and Galilee ($n_{jackals} = 24$, $n_{foxes} = 16$), the Northern valleys ($n_{jackals} = 17$, $n_{foxes} = 18$), the Central region ($n_{jackals} = 15$, $n_{foxes} = 11$), the Northern Negev ($n_{jackals} = 20$, $n_{foxes} = 20$) and the Arava ($n_{jackals} = 12$, $n_{foxes} = 24$) (Fig. 1).

Methods

DNA extraction

DNA was extracted using two methods. Tissue samples were extracted by the guanidinium thiocyanate and silica-based (GuSCN) purification method (Boom et al. 1990; Hoss and Paabo 1993). Blood samples, collected in an EDTA collection tube, were extracted via the phenol–chloroform method (Chomczynski and Sacchi 1987).

DNA amplification, genotyping and sequencing

All samples were genotyped for a set of 14 microsatellites loci (Table 1) developed for the domestic dog (*Canis lupus familiaris*) (Wictum et al. 2012). The tetrameric microsatellite loci used were located on different chromosomes (to avoid linkage disequilibrium) and in non-coding regions. Since the primers sets had been designed based on the domestic dog genome, verification of the microsatellite loci in the golden jackal and red fox was conducted via genotyping and sequencing in a subset of individuals representing these species. Direct Sanger sequencing was conducted on positive amplicons. Sequence chromatograms were then visually inspected to verify the presence of short tandem repeats using Sequencher 4.8 (GeneCorpsInc.).

DNA was amplified for the 14 microsatellite markers through polymerase chain reaction (PCR) using a mixture

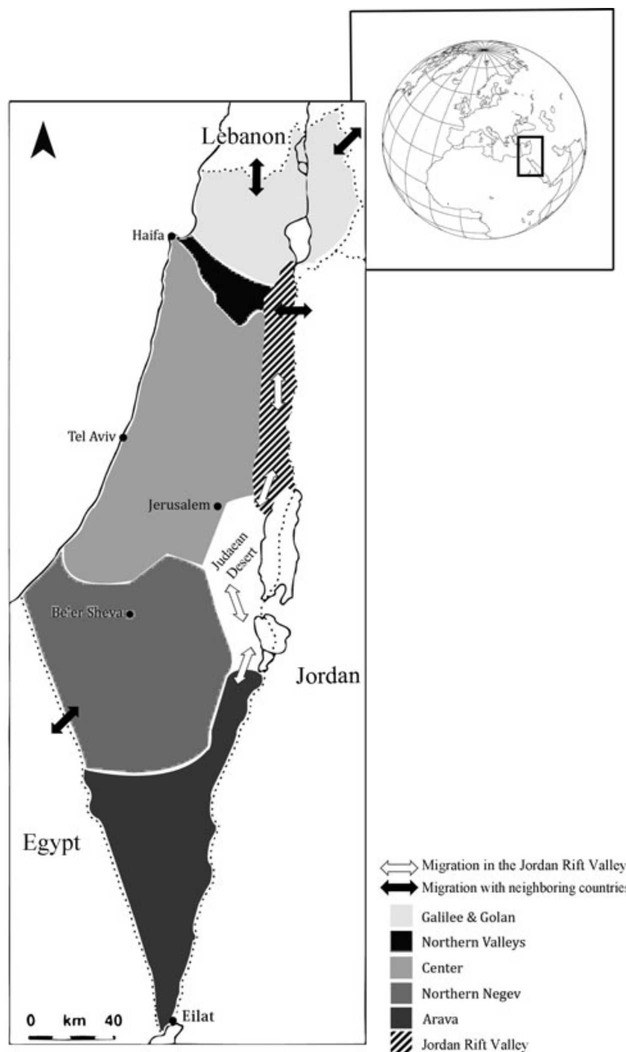

Fig. 1 Map showing the geographic regions into which collected samples were grouped. The geographic regions are designated, from north to south: Galilee–Golan, Northern Valleys, Center, Northern Negev and Arava. *Arrows* indicate likely routes of migration: *black arrows*—migration between neighboring countries, *white arrows*—migration within Israel

that included the following: 2.5 μL PCR buffer, 2.5–3.5 μL $MgCl_2$ (25 mM), 2.5 μL dNTPs (2.5 mM), 1–1.25 μL of each primer (10 μM), and 0.25–0.5 μL AmpliTaq Gold 360 DNA polymerase (Applied Biosystems, Foster City, California, USA). The total volume of the reaction was 25 μL. Polymerase chain reaction was conducted in a thermocycler with a touchdown program as follows: an initial denaturation step at 95 °C for 10 min followed by 45 cycles of 15 s at 95 °C denaturation, 45 s annealing at 60–48 °C, and 45–60 s elongation at 72 °C. Following the 45 cycles, there was a final extension step at 72 °C for 10 min. Genotyping was performed on an ABI PRISM 3700 DNA Analyzer (Applied Biosystems, Foster City, California, USA) at the Center for Genomic Technologies at the Hebrew University of Jerusalem.

Table 1 Microsatellite loci allele size ranges in domestic dog (*Canis lupus familiaris*), golden jackal (*Canis aureus*) and red fox (*Vulpes vulpes*)

Loci	Domestic dog	Golden jackal	Red fox
VGL0760	276–342	283–335	337–469
VGL1063	85–141	101–121	81–127
VGL1165	190–270	190–246	162–202
VGL1541	184–240	183–207	202–298
VGL1606	271–335	280–300	206–346
VGL1828	220–284	239–259	221–263
VGL2009	148–188	162–176	166–198
VGL2136	91–135	102–118	96–104
VGL2409	110–154	125–151	121–163
VGL2918	195–258	203–223	191–215
VGL3008	119–183	124–146	108–124
VGL3112	185–217	181–197	177
VGL3235	270–326	282–294	276–300
VGL3438	136–188	140–152	122–124

Amplicons sizes are listed in bp

Genetic analysis

The ABI software Genotyper, ABI PRISM GeneMapper (Chatterji and Pachter 2006) was used to examine microsatellite alleles and for initial statistical computations. Micro-Checker (Van Oosterhout et al. 2004) was used to look for abnormal allele frequencies, null alleles, and large allele dropouts.

Population genetic analyses were conducted using the software Arlequin 3.5 (Excoffier et al. 2005) and GenAlEx 6.5b2 (Peakall and Smouse 2006). Partitioning of genetic diversity was calculated within and among the subpopulations in both species. Average gene diversity Ha (index of average differences) was determined using Arlequin. Analysis of molecular variance (AMOVA), assignment tests, and fixation indices (the inbreeding coefficient within individuals relative to the subpopulation) were calculated through using the GenAlEx software. Pairwise population differentiation indices F_{st} and Jost's D_{est} were tested by random permutations of 9,999 repeats, calculated in Arlequin and GenAlEx, respectively.

Population structure was examined using the software STRUCTURE 2.4.4 (Pritchard et al. 2000), inferring the most probable number of genetic clusters. The number of clusters (K) was assumed to be between two and ten (*i.e.,* K = 2–10) with each run was repeated three times to examine for deviations among the different runs. A burn-in period of 200,000 followed by 200,000 Markov Chain Monte Carlo (MCMC) repeats for each run and the admixture model with the option of correlated allele frequencies were used along with an additional option of

location prioritization (LOC PRIOR). The LOC PRIOR model was chosen because it uses sampling locations as prior information to assist the clustering of data sets in which the signal is relatively weak. The optimal value of K was chosen by using Evanno's ΔK method (Evanno et al. 2005) implemented in STRUCTURE HARVESTER (Earl and vonHoldt 2012). In addition, biological relevance was also taken into consideration.

In order to examine for evidence of a population bottleneck among the populations of the two species, the program BOTTLENECK version 1.2.0.2 was utilized (Cornuet and Luikart 1996; Piry et al. 1999). Since no prior information regarding the mutation model of the loci used in this study was available, both the two-phase model of mutation (TPM) (Di Rienzo et al. 1994; Primmer et al. 1998) and the SMM model were employed, using 10,000 replicates. The TPM model was run twice, once with 95 % single-step mutations and once with 80 %, with a variance among multiple steps of 12, as recommended by Piry et al. (1999) for datasets analyzed with microsatellites. A one-tailed Wilcoxon signed-rank test was applied to identify gene diversity excess (Luikart 1997) and a qualitative descriptor of the allele frequency distribution ("mode-shift" indicator) was employed to discriminate bottlenecked populations from stable populations (Luikart and Cornuet 1997). Significance levels were adjusted using the Sidak correction: the corrected p value was calculated as the significance level (0.05) divided by the number of loci (13) ($p = 0.004$).

Results

Jackal and fox samples were genotyped at 14 microsatellite loci. The 14 markers demonstrated an average success rate of 93–95 % across the two species. However, for locus VGL1606, low amplification success was observed both in jackals (63.63 %) and in foxes (13.48 %). Therefore, locus VGL1606 was excluded from any further analysis for both species.

In certain loci, allele sizes differed between the two wild canids and differed from those present in the domestic dog (Table 1). All loci were polymorphic among the jackals and all but one locus were polymorphic in foxes. In both species, large numbers of alleles were detected at most loci (Supplementary Table 2), while levels of observed heterozygosity (Ho) and expected heterozygosity (He) were typically within close range of each other (Supplementary Table 2).

Analysis by Micro-Checker detected no signs of large-allele dropouts. However, null alleles were detected among jackals in one locus (VGL3235) across three out of five subpopulations and in two loci (VGL0760 and VGL3008) in three subpopulations among foxes. Consequently, analyses were repeated excluding these loci. However, similar results were obtained for all datasets (with and without these markers) so the markers were included in the final analyses shown.

Clustering analysis

An unbiased method for genetic partitioning into subpopulations was implemented using STRUCTURE 2.4.4. Population information was not considered in this analysis in order to infer the most probable number of genetic clusters without a priori definition of populations. Genotypes from 13 loci were used. Individuals were assigned to one of five geographic regions: Golan Heights and Galilee, Northern valleys, Center, Northern Negev, and Arava. The method of Evanno, combined with biogeographic considerations, suggested that there were five clusters for the jackals (K = 5) and four clusters for the foxes (K = 4) (Fig. 2). The analysis conducted for the foxes indicated that samples from two geographic regions, Galilee–Golan and Northern valleys, had similar patterns of partitioning. Therefore, for further analysis, we combined these two

Table 2 Genetic variability in golden jackals and red foxes determined using microsatellite loci as calculated by GenAlEx

Reported quantities include sample size (*N*), mean number of alleles across loci (*Na*), expected heterozygosity (*He*), observed heterozygosity (*Ho*), fixation index (*F*), and the number of private alleles (*PA*); (*x*) the number of loci, average gene diversity over loci (*Ha*); (*x*) standard deviation

Subpopulation	N	Na	Ho	He	F	PA	Ha
Golden jackal							
Golan Galilee	24	5.643	0.643	0.665	0.029	2 (2)	0.705 (0.366)
Northern valleys	17	5.286	0.660	0.654	−0.006	2 (2)	0.684 (0.354)
Center	15	4.714	0.660	0.651	−0.029	2 (2)	0.717 (0.368)
Northern Negev	20	5.357	0.655	0.687	0.041	2 (2)	0.724 (0.370)
Arava	12	5.214	0.718	0.679	−0.050	1 (1)	0.697 (0.358)
Red fox							
North	34	8.615	0.576	0.592	−0.012	17 (7)	0.629 (0.328)
Center	11	5.000	0.455	0.553	0.166	7 (5)	0.623 (0.335)
Northern Negev	20	6.615	0.571	0.568	−0.040	8 (5)	0.627 (0.330)
Arava	24	6.769	0.486	0.532	0.058	14 (4)	0.579 (0.305)

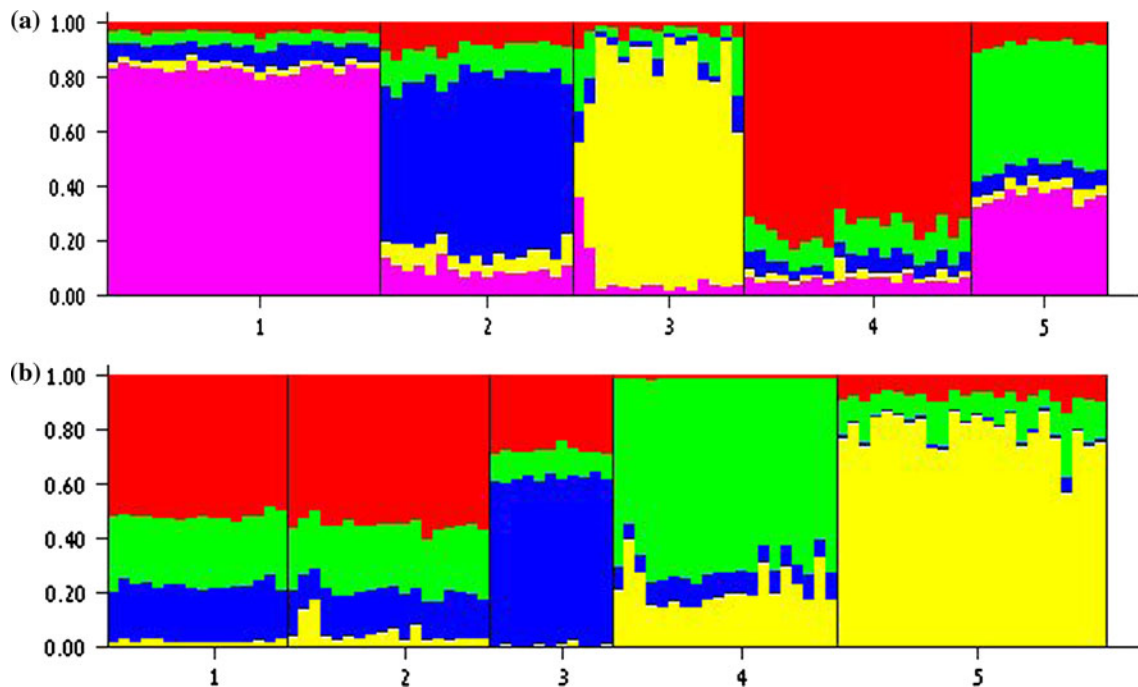

Fig. 2 Bayesian clustering analyses for golden jackals and red fox. Bayesian clustering analyses for golden jackals and red fox, run using the program STRUCTURE 2.4.4, show genotypic clustering by geographic regions for (**a**) golden jackals and (**b**) red foxes. Subdivision into five clusters (K = 5) was supported for the jackals, while four clusters (K = 4) were supported for the foxes. The vertical axis shows the estimated membership coefficients (Q) for each individual in each cluster. Numbers on the horizontal axis represent the geographic origin of the samples as follows: *1* Galilee–Golan, *2* Northern Valleys, *3* Center, *4* Northern Negev, *5* Arava

geographic regions into a single subpopulation for the foxes designating the combined regions the "North" subpopulation.

Having found support for dividing the golden jackal into five subpopulations and the red fox into four subpopulations, we ran assignment tests for both species. Overall, the results of the assignment tests were poor for the jackals. Only 63 % could be correctly assigned indicating that 37 % of the samples were not assigned to their geographic subpopulation of origin. The subpopulation in which the assignment test was most successful (80 % correct) was the Center subpopulation. Interestingly, individuals from the geographically extreme ends of the country (subpopulations Galilee–Golan and Arava) were often mis-assigned to each other suggesting genetic similarities and perhaps a recent biogeographic connection between these geographically distant subpopulations. For example, a sample collected in the Galilee–Golan area was assigned to the Arava subpopulation, approximately 370 km away. In the foxes, 64 % of the samples could be assigned to the correct geographic region of origin. Among the 36 % that were assigned to other subpopulations, 62.5 % (20 of 32 mis-assigned individuals) were instead assigned to a neighboring subpopulation sharing a common boundary. Thus for foxes, genetic similarities supported the occurrence of dispersal or gene flow among proximate geographic regions.

Allele frequencies

Observed and expected heterozygosity among the subpopulations was moderate to high (Table 2) suggesting overall that the subpopulations were genetically diverse perhaps due to gene flow and migration. Fixation index values were from −0.05 to +0.041 for the jackals and from −0.040 to +0.166 for foxes (Table 2). These results indicate that random mating is occurring in both the golden jackal and the red fox populations. In addition, no statistically significant deviations from Hardy–Weinberg expectation were found for loci in either species.

Private alleles (alleles unique to a single subpopulation in the data set) were found in all of the subpopulations in both species (Table 2) with an especially high number of private alleles identified in loci VGL0760 and VGL1541 in the foxes. While a maximum of two loci showed private alleles within any jackal subpopulation, an average of five loci per subpopulation harbored private alleles among the foxes (Table 2). All of the private alleles found were reanalyzed to verify the amplicon size.

Bottleneck test

We searched for the signature of recent bottlenecks using the BOTTLENECK version 1.2.0.2; however, no significant excess heterozygosity was found in jackals or foxes.

Table 3 Tests for genetic signatures of recent population bottlenecks in golden jackal and red fox populations in Israel

	TPM				SMM		
	Proportion of SMM in TPM (%)	Wilcoxon sign rank test probability		Mode shift	Wilcoxon sign rank test probability		Mode shift
Population		One tail for H deficiency	One tail for H excess		One tail for H deficiency	One tail for H excess	
Golden jackal	95	0.52698	0.50000	Normal L-shaped distribution	0.1698	0.84729	Normal L-shaped distribution
	80	0.91614	0.09546				
Red fox	95	0.04016	0.96594	Normal L-shaped distribution	0.00116	0.99915	Normal L-shaped distribution
	80	0.22742	0.79285				

Numbers reported are p values of Wilcoxon sign-rank tests under the SMM and the TPM models implemented using the program BOTTLENECK. The TPM model was evaluated twice, assuming: (1) 95 % single-step mutations (2) 80 % single-step mutations. Values in bold failed to reject the null hypothesis of a recent bottleneck ($p < 0.004$; Sidak correction)

The Wilcoxon signed-rank tests found no evidence of a bottleneck in either of the species (Table 3). However, while there was no significant excess heterozygosity in either species, a significant deficit of heterozygotes was found in the foxes under the single-step (SMM) model ($p < 0.004$; Sidak correction). In contrast, neither species demonstrated significant heterozygosity deficit under the TPM model ($p > 0.004$; Sidak correction).

Genetic diversity

Gene diversity (Ha) calculated across all loci was similar among most subpopulations in both species (Table 2), indicating high genetic diversity within subpopulations. When genetic diversity was calculated between subpopulations, the mean F_{st} value was 0.051 in jackals and 0.043 in foxes, suggesting a total genetic variation of 4–5 % across subpopulations (data not shown).

The Center subpopulation in both species differed from other subpopulations with values higher than seen among most other comparisons (Table 4). Overall, the remaining four subpopulations displayed low generic differentiation indicating greater gene flow between individuals from neighboring subpopulations. A unique pattern appeared in the jackals in which the Galilee–Golan subpopulation was most closely related to the Arava subpopulation although these two populations were the most distant from each other (~370 km) (Fig. 1).

Table 4 Genetic differentiation and distance between golden jackal and red fox populations based on genotypic frequencies using microsatellite loci

Golden jackal

	Golan Galilee	Northern valleys	Center	Northern Negev	Arava
Golan Galilee		0.036	0.057	0.039	0.034
Northern valleys	0.062		0.063	0.047	0.058
Center	0.110	0.105		0.067	0.062
Northern Negev	0.075	0.081	0.138		0.050
Arava	0.030*	0.081	0.096	0.066	

Red fox

	North	Center	Northern Negev	Arava
North		0.046	0.009*	0.032
Center	0.025		0.051	0.090
Northern Negev	0.018	0.045		0.027
Arava	0.051	0.083	0.036	

Above the diagonal: D_{est}values; below the diagonal: F_{st} values

* Not significant ($p > 0.004$; Sidak correction)

Discussion

This is the first study of the genetic characteristics of golden jackal and red fox populations in Israel, and one of only a few studies to focus on genetic aspects of the golden jackal globally (Bardeleben et al. 2005; Zachos et al. 2009). Applying molecular genetic tools has made it possible to gain greater knowledge of the current status of these populations in Israel and to harness this information to develop efficient management strategies that may be of assistance in wildlife conservation.

The primers used in this study were adapted from the domestic dog (Wictum et al. 2012) as all three species are of the family Canidae. Phylogenetically, the golden jackal is more closely related to the domestic dog than the red fox (Wayne et al. 1997; Bardeleben et al. 2005). Both species displayed some loci with microvariant and out-of-range

alleles compared to domestic dogs, while four loci exhibited fewer than three alleles per locus in foxes, including one STR locus that was monomorphic (Table 1).

Bayesian clustering analysis of genotypes for both species suggested that five subpopulations could be discerned among the jackals and four among the foxes (Fig. 2). Values of F_{st} or D_{est} were generally low between geographically adjacent subpopulations, but were higher in comparisons involving the Center subpopulation (Table 4) suggesting the genetic isolation of canids in this region. In addition, assignment tests conducted on the jackals and foxes yielded low values for the accurate assignment of individuals to their correct sampling region (63 % in jackals and 64 % in foxes) supporting close genetic affinities across the subpopulations. This may be a result of high gene flow or dispersal of individuals since juvenile golden jackals and red foxes leave their social unit and migrate to the margins of their natal territory (Jhala and Moehlman 2004; Macdonald and Reynolds 2004; Sillero-Zubiri et al. 2004).

The lack of major geographical and anthropogenic barriers along the Jordan Rift Valley (as opposed to the Center region) makes it a likely candidate for dispersal of jackals and foxes from the north to the south and vice versa. This is supported by the relatively higher F_{st} or D_{est} values estimated between the Center and other subpopulations (Table 4). This directional dispersal may help to explain why, despite not being present in the southern parts of Israel prior to the 1964 eradication program, jackals have since invaded the south extending to Israel's most southern border (Nemtzov 2002). The expansion of the potential range of the jackal may also have been enabled by anthropogenic changes, such as the increase in human settlements in the area in the past 30 years (Central Bureau of Statistics 2010).

Additional crossings are likely to occur from the east to the west from the Jordanian side of the Jordan Rift Valley inward. Although little information is available regarding these species in Jordan, certain areas along the Jordan Rift Valley, especially in the Jordan territory, are rich with food sources and human settlements, and an abundance of jackals in these areas has been documented before by Mendelssohn (1972) While the lack of samples from Jordan cannot allow for testing of the hypothesis that cross-border gene flow and migrations occur, ecologically there are no boundaries that would prevent canids from moving between the two countries.

The Center subpopulation is distinct in both species (Table 4). The relative isolation of the Center subpopulation may in part be due to food availability. Abundant food resources are available to jackals and foxes in the Center area of Israel due to excessive human development (Bino et al. 2010), which may lead to a relative reduction in dispersal to the nearby subpopulations (Dolev 2006). Additionally, migration in and out of the Center subpopulation may be limited for both jackals and foxes by the higher density of roads in the region. A study on the impact of motor vehicle traffic in Israel on wildlife has found that jackals are at the highest risk and foxes at third highest risk to be killed especially along the major highways (Gutman et al. 2002 Roads may limit the immigration and emigration of canids in the Center subpopulation due to road kills and to limited dispersal across roads.

All subpopulations of both the golden jackal and the red fox were found to be highly genetically diverse as expressed in high average gene diversity measures as well as expected and observed heterozygosity values (Table 2; Supplementary Table 2). In addition, the close-to-zero fixation index values were indicative of outbreeding and random mating suggesting that the populations of both species are not isolated (Frankham 2005).

In the absence of pre-bottleneck diversity data for the jackal, genetic patterns in the jackal was compared to those of a related species (Frankham 1995), the red fox. Both species were found to be highly genetically diverse (Supplementary Table 2) and similar patterns could be inferred for geographic partitioning and gene flow (Table 4). Genetic diversity would have been expected to decrease in a population that has gone through a severe bottleneck such as the one experienced by the golden jackal (Ellengren et al. 1993; Hoelzel et al. 1993; Frankham and Ralls 1998). Yet our results indicate that the golden jackal population has reached a level of genetic diversity comparable to that of the red fox, which did not undergo a bottleneck (Chevolot et al. 2008). Moreover, the software Bottleneck found no evidence of a recent bottleneck in either species (Table 3). In addition to gene flow across subpopulations within Israel, additional gene flow with populations from neighboring countries such as Jordan, Syria, and Lebanon is highly likely based on the distribution of habitats. The high genetic diversity found among jackals even after the recent bottleneck strongly suggests that immigration from neighboring countries accelerated the rate of genetic recovery after the poisoning campaign ended (Berthier et al. 2006). The high dispersal ranges of the golden jackal (Sillero-Zubiri et al. 2004) would also have facilitated this recovery (Frankham et al. 2002).

Implications for conservation

This study includes samples from most major regions in Israel and is exceptional in the geographic extent of sampling. Golden jackals and red foxes are both protected under Israeli law, yet are also considered agricultural pests. Management of these species is often tentative and relies on periodic population counts held by the INPA (Nemtzov 2002). The current management program relies on defining

a source population and its margins assuming that when a habitat is saturated, dispersing individuals are responsible for much of the agricultural damage and the spread of rabies (Nemtzov and King 2002). Management actions are executed on this basis.

Until the present study, neither golden jackal nor red fox populations had been characterized genetically and the geographic delimitations of subpopulation were unclear. The possibility that Israeli subpopulations are interacting with those of neighboring countries suggests the need to characterize their populations and determine their role and impact on the Israeli subpopulations. Understanding the structure of populations of both species may aid in future management both for conservation and to limit their impacts on agriculture.

Our major finding of a route of dispersal through the Jordan Rift Valley and the likely migration of specimens from neighboring countries into Israel may suggest general geographic routes of dispersal for native or invasive species in Israel. It may also indicate the routes likely to be taken by pathogens carried by dispersing animals, including potentially a new rabies strain currently restricted to the northern parts of Israel (David et al. 2009). As frequent contacts between adjacent resident groups may affect rabies transmission (Macdonald and Voigt 1985; White et al. 1995) precautions must be taken in order to alleviate the prevention of the spread of the disease, preferably before the virus has penetrated into more regions in Israel. The possibility of long-distance transmission of rabies from northern Israel directly into southernmost Israel must also be considered, given that genetic patterns suggested high migration rates for wild canids between northern and southern Israel.

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